

ZOOGEOGRAPHY AND SYSTEMATICS OF SIX
DEEP-LIVING GENERA OF SYNAPHOBANCHID
EELS, WITH A KEY TO TAXA AND
DESCRIPTION OF TWO NEW
SPECIES OF *ILYOPHIS*

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ABSTRACT

An extensive series of deep-sea synphobranchid eels was studied, primarily from previously unreported Russian collections in the southern Indian and southwestern Pacific oceans. Together with previous records, new Russian records provide a worldwide summary of the geographic and bathymetric distributions of the 14 species comprising the genera *Diastobranchus*, *Haptenchelys*, *Histiobranchus*, *Ilyophis*, *Simenchelys*, and *Synphobranchus*. A diagnostic key defines species in these genera, including two newly discovered species of *Ilyophis*. The multi-character key facilitates unequivocal identification of synphobranchid specimens. *Diastobranchus* and *Histiobranchus* are re-established as genera distinct from *Synphobranchus*. Diagnoses of subfamilies and genera are refined. The zoogeography of studied taxa is summarized.

Synphobranchid eels are important components of the demersal deep-sea fish fauna at continental slope and rise depths in both temperate and tropical regions. Indeed, in all well-sampled regions except the northeastern Pacific, they have consistently proven to be a dominant fraction of the bathyal fish fauna in terms of relative abundance from bottom trawl samples (Markle and Musick, 1974; Haedrich et al., 1975, 1980; Merrett and Marshall, 1981; Sulak, 1982; Gordon and Duncan, 1985; Merrett and Domanski, 1985; Gordon, 1986). Off the northern Mid-Atlantic coast of the U.S. synphobranchids made up 10–14% of all demersal fishes obtained in 12.2-m otter trawls between 1280 and 1960 m depths (Haedrich and Horn, 1970; Haedrich and Polloni, 1974), 53% in 4.9-m trawls between 393–1095 m (Haedrich et al., 1975) and 21% of all megafauna (fishes and benthic invertebrates) from three trawl types between 653–1290 m (Haedrich et al., 1980). Along the Mid-Atlantic coast of the U.S. synphobranchids constituted 19–43% by number of all demersal fishes obtained in 13.7-m otter trawl samples between 1350 and 1908 m depths; in the Bahamas, 34–47% between 1440 and 2350 m depths (Sulak, 1982). In the Rockall Trough region of the northeastern Atlantic *Synphobranchus kaupii* ranked as the third to first most abundant species (7–41% by number) captured at four depth horizons between 750–1500 m in small-mesh Agassiz trawls (Gordon and Duncan, 1985). Between 800–1200 m off southeastern Australia *Diastobranchus capensis* accounted for 39% of fishes obtained in 35–37 m commercial trawls (Koslow et al., 1994). Nonetheless, knowledge of biology of the Synphobranchidae has remained rather poorly developed, while the systematics and zoogeography of the family have received primarily regional treatment. The present study presents a worldwide synopsis of species identities and distributions for six of the 11 synphobranchid genera, including 14 species of deep-living synphobranchid eels.

Despite its apparent ecological importance to the demersal deep-sea fauna, the Synphobranchidae displays limited morphological and probably trophic diversity. Only 29 species comprise this anatomically conservative eel family. Moreover, in no given geographic and bathymetric zone do more than two species of syna-

phobranchid eels co-occur as faunal dominants. This contrasts, for example, with the Macrouridae, a family which is both speciose and represented by many co-occurring species (often co-dominants) in most regions and depths.

Three subfamilies of Synaphobranchidae are currently recognized (Robins and Robins, 1989), the Synaphobranchinae, Simenchelyinae and Ilyophinae. Four illyophine genera, *Atractodenchelys*, *Dysomma*, *Dysommima* and *Meadia*, are primarily inhabitants of the upper to middle slope (200–1000 m), and are poorly represented in collections utilized in the present study. No specimens of the recently described *Thermobiotes* were examined. These five genera are not treated herein. However, the first four have been summarized by Robins and Robins (1989); *Thermobiotes* by Geistdoerfer (1991). With the addition of two subsequently described species (Mok et al., 1991; Chen and Mok, 1995), these genera comprise 14 species. The remaining six genera considered herein, *Diastobranchus*, *Haptenchelys*, *Histiobranchus*, *Ilyophis*, *Simenchelys*, and *Synaphobranchus*, comprise an additional 14 species worldwide. The geographic ranges of most species in these genera are very broad, necessitating systematic comparison and distributional summary on a global scale.

The present study combines data from a large series of synaphobranchid eels from Russian collections (see Appendix), from regional faunal studies conducted off Virginia and the Bahamas (Sulak, 1982), from the literature, and from unpublished data. Most new records have come from Russian sampling in the Southern Hemisphere, primarily in the southern Indian and southwestern Pacific oceans. Together with other reliable locality records, new Russian records have enabled a worldwide summary of the geographic and bathymetric distributions of species in the six genera studied. Several of the species treated have previously been known from rather few records or from a limited geographic region.

Identification of synaphobranchid species is often technically challenging, especially with damaged specimens (frequently the case with bottom trawl material), or in the absence of comparative study material. Single character state dichotomies of the type given in conventional keys, not backed up by supplementary characters, often do not enable unequivocal species identification. Thus, a simple dichotomous key is inappropriate for identification of synaphobranchid eels. Species are best distinguished based on a suite of external characters, with confirmation when necessary (rarely) based on vertebral counts. Accordingly, a new diagnostic key has been constructed which relies primarily on multiple definitive external characters, but also incorporates other supplementary characters including vertebral counts. The new key takes into account two newly discovered species of *Ilyophis*, and new data from Indo-Pacific specimens of previously described species. Geographic and bathymetric ranges useful in delineating the most probable species for a particular region and depth zone are also given.

Knowledge of the zoogeography of synaphobranchid eels has been hampered by uneven sampling effort and regional treatments in the literature. The distribution of each species studied is summarized as fully as possible with respect to geography, bathymetry and temperature.

METHODS AND MATERIALS

Systematics.—Material in Russian collections was examined at the Zoological Institute, Russian Academy of Sciences, Leningrad; the Zoological Museum, Moscow State University, Moscow; the Institute of Oceanology, Russian Academy of Sciences, Moscow, and at sea during Cruise 17 of the research vessel VITIAZ in the southwestern Indian Ocean. A list of all primary taxonomic study material is presented in the Appendix. Terminology of cephalic lateralis canals derives from Allis (1888) for *Amia*, except for our addition of the new term “supraorbital branch”, and use of “temporal canal”

Table 1. Geographic distribution of total vertebral counts (range with number of specimens in parentheses) for four species of synphobanchine eels. Data is from the present study and literature sources. Key to regions: WNA = western North Atlantic, WSA = western South Atlantic, ENA = eastern North Atlantic, ESA/SWIO = eastern South Atlantic and southwestern Indian Ocean, Gulf of Guinea to Mozambique Channel, CEIO = central and eastern Indian Ocean, WNP = western North Pacific, WSP = western South Pacific, ENP = eastern North Pacific, WSP = western South Pacific.

Region	Species			
	<i>S. affinis</i>	<i>S. oregoni</i>	<i>S. kaupii</i>	<i>H. bathybius</i>
WNA	129–136 (33)	142–148 (24)	147–150 (4)	137 (1)
WSA	—	—	—	—
ENA	—	—	146–149 (3)	—
ESA/SWIO	132–139 (11)	130 (1)	144–148 (2)	122–131 (18)
CEIO	127–131 (2)	130–137 (4)	—	132–138 (7)
WNP	143–150 (2)	132 (1)	141–148 (6)	136 (2)
WSP	135–137 (3)	127–129 (5)	—	126–137 (6)
ENP	146 (1)	—	—	129 (1)
ESP	131–135 (2)	—	—	—

(following Smith, 1989b) in lieu of the cumbersome "postotic segment of the cephalic canal." Numbering sequence for canal pores follows Trotti (1940), except that pores in the temporal canal series are not counted as a continuation of the preopercular-mandibular canal series. Museum acronyms follow Leviton et al. (1985), with one addition and two modifications as follows: IOS = Institute of Oceanographic Sciences, Deacon Laboratory, Wormley, Godalming, Surrey, England; ZIL = Zoological Institute, Leningrad; ZMMU = Zoological Museum, University of Moscow. Abbreviations used are as follows: ED = horizontal orbit diameter; HL = head length; IOC = infraorbital canal; LGA = length of gill slit; LL = lateral line, LLA = lateral-line pores to level of anus; LLT = lateral-line pores to posterior end of lateral-line tubule; PA = preanal length—tip of snout to origin of anal fin; PD = predorsal length—tip of snout to origin of dorsal fin base; PL = length of pectoral fin; PMC = preopercular-mandibular canal; PME = premaxillary-ethmoid toothpatch, PO-LL = interspace between posterior margin of orbit and first trunk lateral-line pore, SNL = snout length, SB = supraorbital branch of supraorbital canal; SOC = supraorbital canal; STC = supratemporal cross-commissure canal; TS = temporal canal pore series; TL = total length, TV = total vertebrae, VO = vomerine toothpatch. Cant of hyomandibula (vertical, anteriorly canted, or posteriorly canted) was determined by angle (right, acute, or obtuse) formed between the upper portion of the median ridge (bony canal) of the hyomandibula and the long axis of the parasphenoid.

Radiography was limited to a small number of specimens due to the prohibitive cost of X-ray film. However, our data, together with literature data, enabled a first-order synopsis of comparative regional distribution of total vertebrae counts for four broadly distributed species (Table 1).

Zoogeography.—Plots of species distributions are based on material examined in the present study, extensive material previously identified by the authors (Sulak, 1982), and verifiable literature records. Records included in our synopses and distribution plots derive from published and unpublished material collected up to 1991, with a few subsequent additions. Recent records from off southeastern Australia (Koslow et al., 1994) and off New Caledonia (material under study by senior author, MUSEORSTOM Project, Museum National d'Histoire Naturelle, Paris) are acknowledged by us, but are not included the present study. Distribution plots, as well as analyses of size, depth, and latitude relationships, were based on the complete locality record database of species records accepted as valid by us, and maintained by the senior author.

RESULTS AND DISCUSSION

Systematics.—Counts of TV and LLA are based only on specimens examined in the present study (except for *H. bruuni* data from Castle, 1964, 1968). Depth data are derived from the overall database of accepted locality records.

**DIAGNOSTIC KEY TO SPECIES OF SYNAPHOBANCHID
EELS OF THE DEEP-LIVING GENERA *DIASIOBRANCHUS*,
HAPTENCHELYS, *HISTIOBRANCHUS*, *ILYOPHIS*,
SIMENCHELYS, AND *SYNAPHOBANCHUS***

- 1A. Head thick, blunt, cylindrical (Fig. 1A); mouth very small and terminal, gape falling well short of orbit; less than 20 teeth in each jaw, set in a single row; lips strongly plicate around circumference of slit-like mouth; hyomandibula canted distinctly anteriorly; TV 118–122; gill slits broadly separate; cephalic lateralis system reduced; body scaled in grouped, right-angle basketweave pattern; TL to 585 mm subfamily *Simenchelyinae*, genus *Simenchelys* ... monotypic ... *Simenchelys parasitica*¹ Gill, in Goode and Bean, 1879, bi-temperate, circumglobal, except eastern northeastern Pacific, 136–2620 m.
- 1B. Head slender, pointed, conical; mouth large, gape extending to or beyond orbit; jaw teeth numerous, set in multiple rows or in a broad band; plicae when present restricted to tips of jaws; TV 122–188; hyomandibula vertical or variously canted 2
- 2A. Toothed tip of lower jaw projecting beyond that of upper jaw (jaws approximately equal in *Haptenchelys*); gape upturned in lateral profile with mouth closed; tip of snout without distinct plicae (except *Haptenchelys*) or papillae; pectoral fin longer than ca 50% gape length (except *Haptenchelys* and *Histiobranchus*); eye large, ED less than 2.5 times into SNL (except *Haptenchelys*); PO-LL shorter than SNL (except *Haptenchelys* and *Histiobranchus*); hyomandibula strongly canted posteriorly; gill slits either confluent or separated by an interspace distinctly shorter than gill slit length (except *Haptenchelys*); VO either with no enlarged teeth or only a few anteriorly; PME and VO separated by an interspace greater than one-half PME length (except *Haptenchelys*); SOC series complete, 5–7 pores (except *Haptenchelys*); SB and STC with pores (except *Haptenchelys* and *Histiobranchus*) subfamily *Synaphobranchinae* ... 7
- 2B. Toothed tip of upper jaw projecting distinctly beyond that of lower jaw (except nearly equal in *I. arx* and *I. robbinsae*); gape straight in lateral profile with mouth closed; tip of snout distinctly ornamented with plicae and/or papillae; pectoral fin shorter than 50% gape length (except in *I. arx*); eye small, ED 2.5 times or more into SNL; PO-LL considerably longer than SNL (except equal in *I. arx*); hyomandibula vertical or slightly canted anteriorly or posteriorly; gill slits always separated by an interspace longer than gill slit length; dorsal fin origin over or slightly behind pectoral fin; VO usually bearing a median series of enlarged teeth; PME and VO in contact or separated by a very narrow interspace (shorter than one-half PME length); SOC with 3–6 pores, usually incomplete; SB and STC with or without pores subfamily *Ilyophinae* (in part)² ... genus *Ilyophis* ... 3
- 3A. Cephalic lateralis system with full complement of pores (Fig. 1B–C)—SOC with 6 pores—3 lying above the orbit, SB with 1–2 pores, STC with 2–3 pores; posterior nostril partially occluded by a distinct flap anteriorly (Figs. 1B–C, 2A); inside corner of gape reaching only to posterior margin of orbit “*blachei*” species group 4
- 3B. Cephalic lateralis system with reduced number of pores (Figs. 3A–C)—SOC with only 2–4 pores, restricted to the snout region, none lying above the orbit; SB and STC without pores; posterior nostril a simple, smooth-rimmed aperture without a prominent flap (Figs. 3A–C); inside corner of gape extending beyond orbit by 0.5–2.0 ED “*brunneus*” species group 5
- 4A. Flap of posterior nostril broad, angular; flap and nostril rim ornamented with numerous leaf-like marginal projections (Fig. 2A); gill slits very oblique (ca 30° relative to horizontal body axis) (Fig. 1B); TV 177–188; LLA 37–44, LLT 160–170; LL tubule reaching nearly to tip of tail; body either partially scaled or naked; hyomandibula distinctly canted anteriorly; a large, robust species, TL to 792 mm *Ilyophis blachei* Saldanha and Merrett, 1982, bi-temperate, northeastern Atlantic and austral, 580–2023 m.
- 4B. Flap of posterior nostril lunate, flap and nostril rim fairly smooth, ornamented with small marginal papillae only (Fig. 2B); gill slits horizontal to slightly oblique; TV 141–147; LLA 32–37, LLT 85–92; LL tubule ending well short of tip of tail (LL tubule length 70–80% TL); completely scaled (except abdomen) in irregular right-angle pattern; 1–6 long scales per group, length:width ratio variable, 3:1 to 10:1; hyomandibula vertical or slightly canted anteriorly; a slender species, TL to 513 mm *Ilyophis nigeli* n. sp., Pacific, off Japan, 700–1780 m.

¹ The Greek ending “enchelys” (meaning “eel”) in the generic name is feminine, necessitating a feminine ending in the adjectival specific name “*parasitica*”.

² Diagnosis of subfamily *Ilyophinae* in the present key is based only on species of *Ilyophis*, and may not apply to species of the remaining genera, *Atractodenchelys*, *Dysomma*, *Dysommima*, *Meadia*, and *Thermobiotes*.

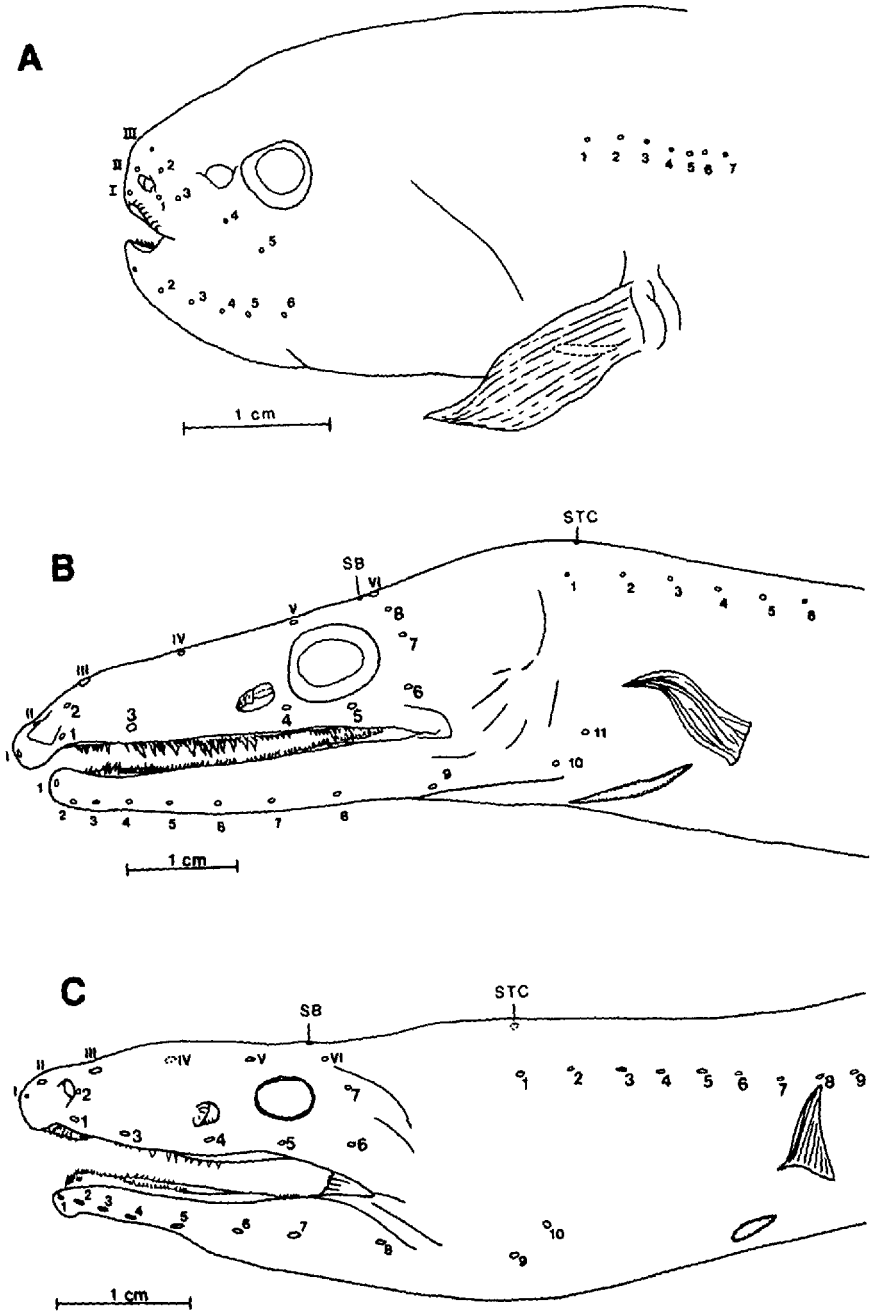


Figure 1. Cephalic morphology and lateralis system in: A—*Simenchelys parasitica*, ARC uncataloged; B—*Ilyophis blachei*, USNM 315198; C—*Ilyophis nigeli* n. sp., ZIL 45767. Supraorbital canal pores designated with Roman numerals; infraorbital, preopercular-mandibular, and body lateral line with Arabic numerals.

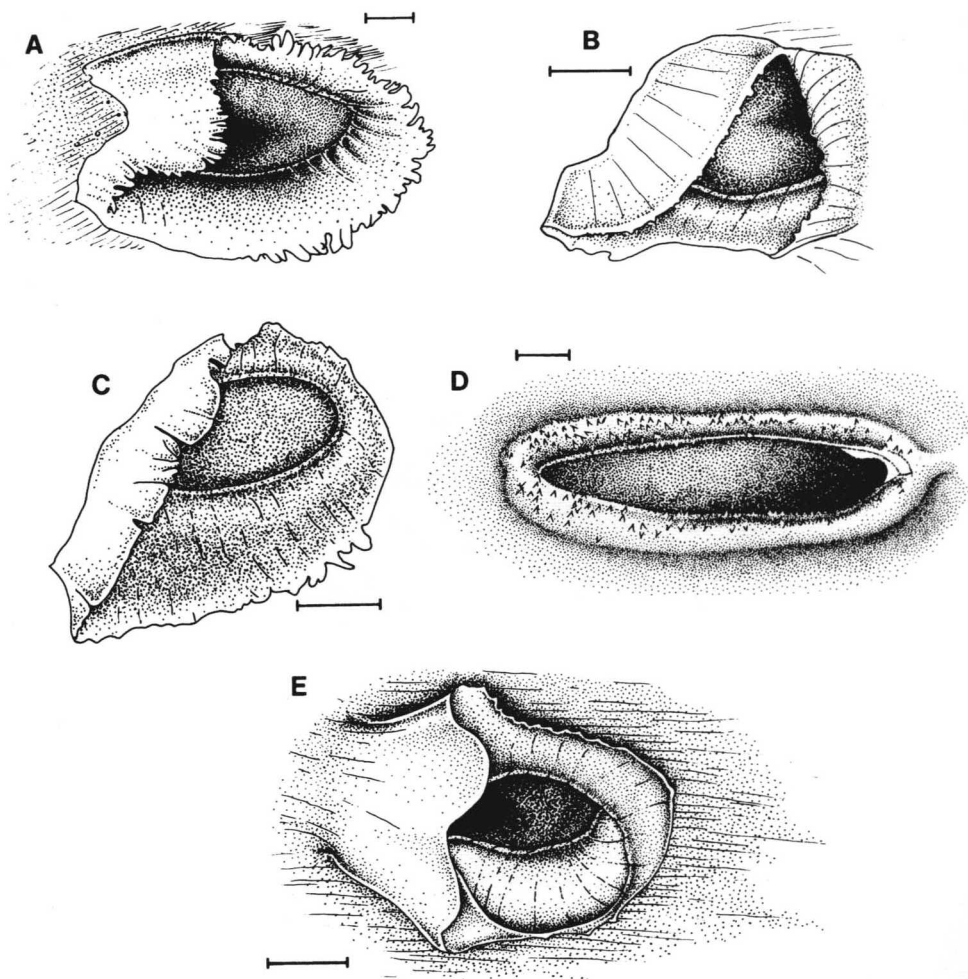


Figure 2. Posterior nostril (anterior end to the left) in: A—*Ilyophis blachei*, USNM 315198; B—*Ilyophis nigeli* n. sp., ZIL 45767; C—*Diastobranchius capensis*, ZMMU 16271; D—*Haptenchelys texis*, ANSP 133812; E—*Synaphobranchus kaupii*, ARC 8705146. Scale bars = 0.5 mm.

- 5A. Parietal-occipital region swollen into a characteristic "bump" behind the eyes (Fig. 3A); toothed tip of upper jaw noticeably extending beyond tip of lower jaw; PME with 6 enlarged plus 16 smaller teeth (Fig. 4A); LL pores typically white and exceptionally distinct; completely scaled in regular, grouped, right-angle pattern; 3–7 long scales per group, length: width ratio approximately 8:1; gill slits horizontal or slightly oblique; snout ornamented with 3–4 simple plicae; slender; TV 140–154; LLA 33–38; LLT 99–123; TL to 637 mm . . . *Ilyophis brunneus* Gilbert, 1892, circumtropical—except northeastern Pacific, 450–3120 m.
- 5B. Parietal-occipital region without a distinct swelling; toothed tip of upper jaw not extending or barely extending beyond tip of lower jaw; variously completely scaled, scaled in irregular patches, or naked 6
- 6A. Head blunt, snout short and deep (Fig. 3B), plicae few but complex; all teeth in jaws small and uniform in size; club-shaped PME with 19–23 similar, but enlarged teeth; VO with 9–11 enlarging teeth arrayed marginally and irregularly in a double row; pectoral fin much longer than gill slit (Fig. 3B), its base nearly equal in length to and lying directly opposite gill slit; 15 pectoral rays; either patchily and irregularly scaled or naked; gill slits horizontal or slightly oblique; TV 131–135; LLA 26–30; LLT ca. 80; TL to 447 mm *Ilyophis arx* Robins and Robins, 1976, tropical eastern Pacific and northeastern Atlantic, 1790–3225 m.

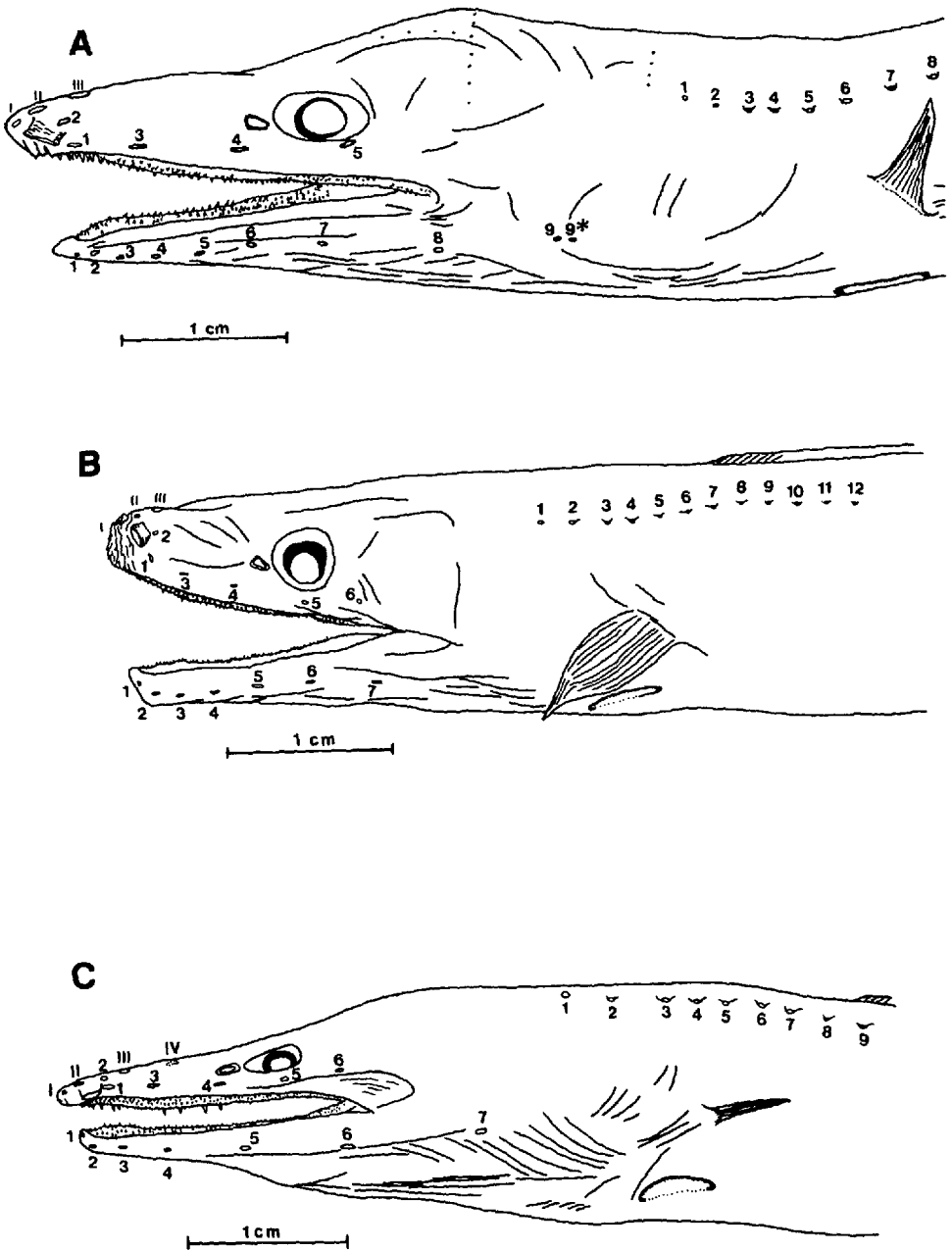


Figure 3. Cephalic morphology and lateralis system in: A—*Ilyophis brunneus*, ZIL 43822 (* = supernumerary pore); B—*I. arx*, IOS, DISCOVERY Collection, Station 50710; C—*I. robinsae* n. sp., ZMMU 17459.

6B. Head long and conical, snout tapering to a fine point (Fig. 3C), plicae simple—rather poorly developed compared to other species of *Ilyophis*; PME with 6 enlarged plus 45 small teeth (Fig. 4B); VO with a row of enlarged teeth medially; pectoral fin small and slender, only slightly longer than gill slit (Fig. 3B), its origin over posterior part of slit; 11 pectoral rays; pores on head and in LL large and distinct; naked; gill slit horizontal; TV 141; LLA 31; LLT 87; TL to 616 mm *Ilyophis robinsae* n. sp., Indo-West Pacific, 4800 m

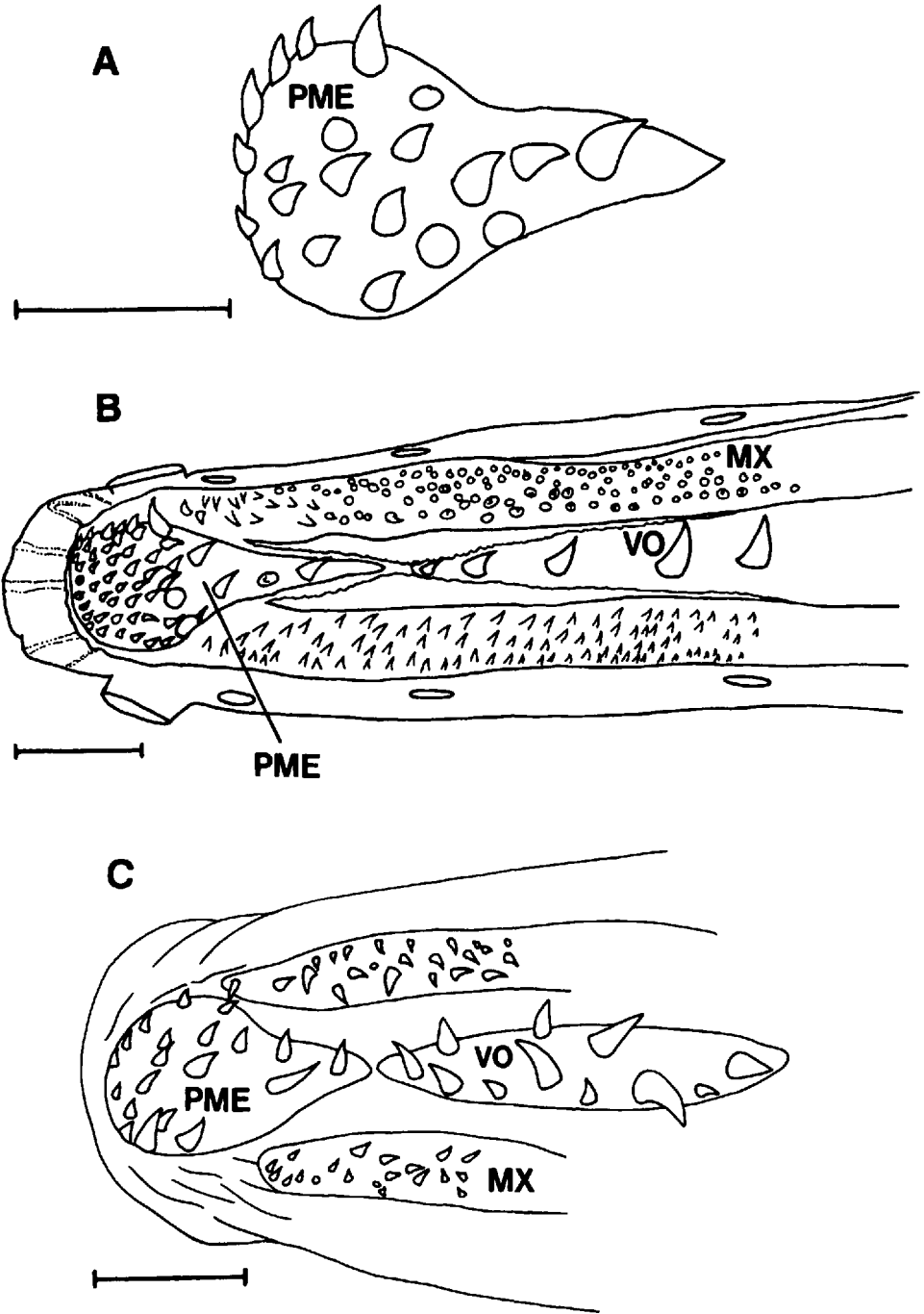


Figure 4. Dentition on the palate in: A—*I. brunneus*, ARC 8704395; B—*I. robinsae* n. sp., ZMMU 17459; C—*Ilyophis nigeli* n. sp., ZIL 48482. Key: MX = maxillary toothpatch, PME = premaxillary-ethmoid toothpatch, VO = vomerine toothpatch. Scale bar = 2 mm.

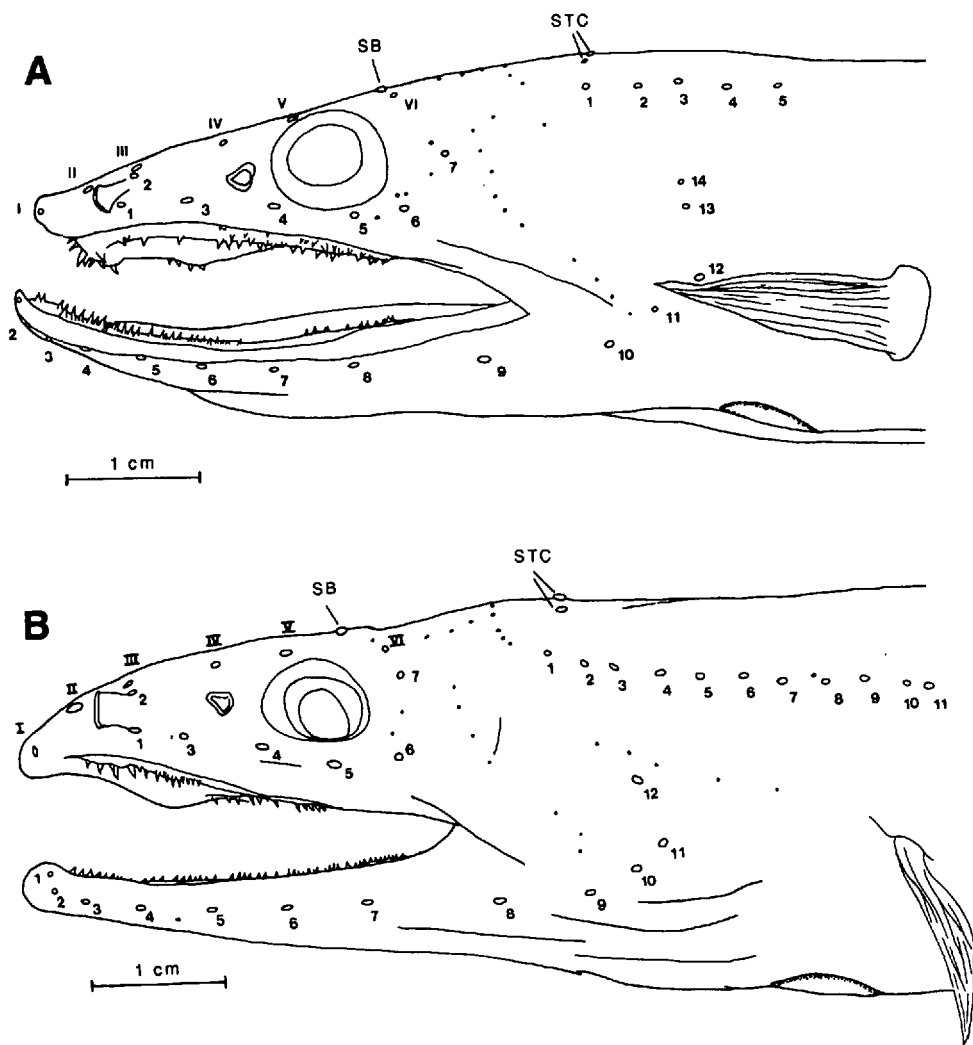


Figure 6. Cephalic morphology and lateralis system in: A—*Synaphobranchus brevidorsalis*, ARC 8909796; B—*S. oregoni*, ARC 8909794.

teeth; tip of snout with a few simple plicae; LLA 31-35; LLT ca 65; TL to 511 mm; TV 125-132 genus *Haptenchelys*, monotypic ... *Haptenchelys texis* Robins and Martin, in Robins and Robins, 1976, amphi-Atlantic, 2121-4086 m.

- 9A. Pectoral fin falciform and long, length exceeding gape length; no TS pores, SB with one pore, STC with 2-3 pores (Fig. 7B); only one postorbital pore in IOC; PO-LL shorter than SNL; dorsal fin origin far behind pectoral fin and anal fin; anal fin origin far forward, no more than one PL behind that fin; PME and VO separated by a space exceeding one-half PME length (Fig. 8E), VO with a terminal group of 2-4 large canine teeth anteriorly, PME oval; LLA less than 30; pterygoid intact, articulating with both quadrate and premaxillary-ethmoid; completely scaled in regular, grouped, right-angle basketweave pattern (Fig. 9E); 5 or more long scales per group, length:width ratio 6:1 or greater; gill slit oblique, posterior end adjacent to pectoral fin base; tip of snout smooth, without plicae or distinct papillae; color black; attains large size, TL to 1250 mm; TV 164-168 genus *Diastobranchus*, monotypic

Diastobranchus capensis Barnard, 1923, circum-austral—except eastern Pacific, 183-1750 m.

- 9B. Pectoral fin rounded, PL shorter than one-half gape length; TS with 3 pores in a lateral

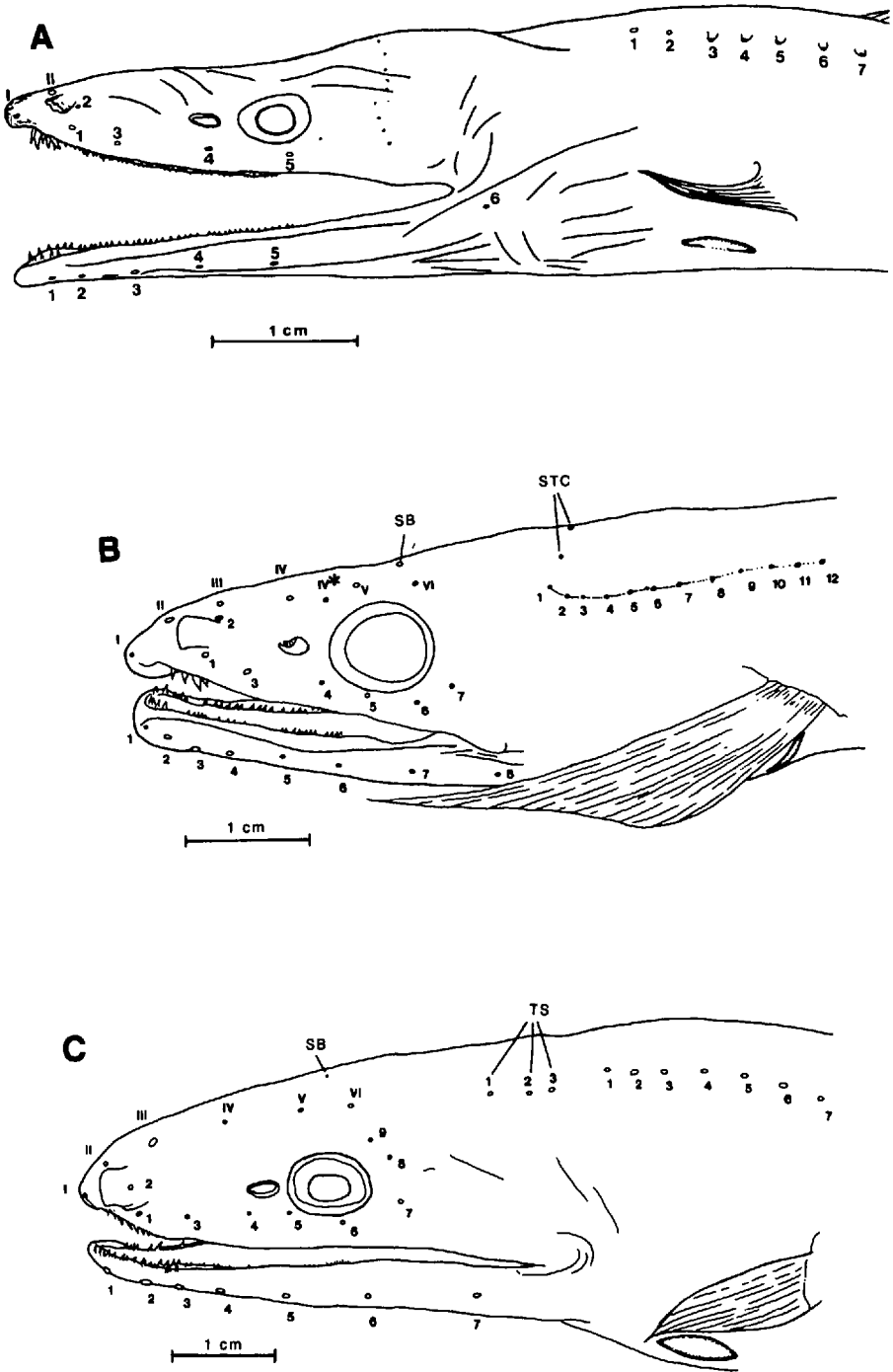


Figure 7. Cephalic morphology and lateralis system in: A—*Haptenchelys texis*, IOS, DISCOVERY Collection, Station 8682#5 (* = supernumerary pore); B—*Diastobranchus capensis*, ZMMU 16271; C—*Histiobranchus bathybius*, ARC 8909793.

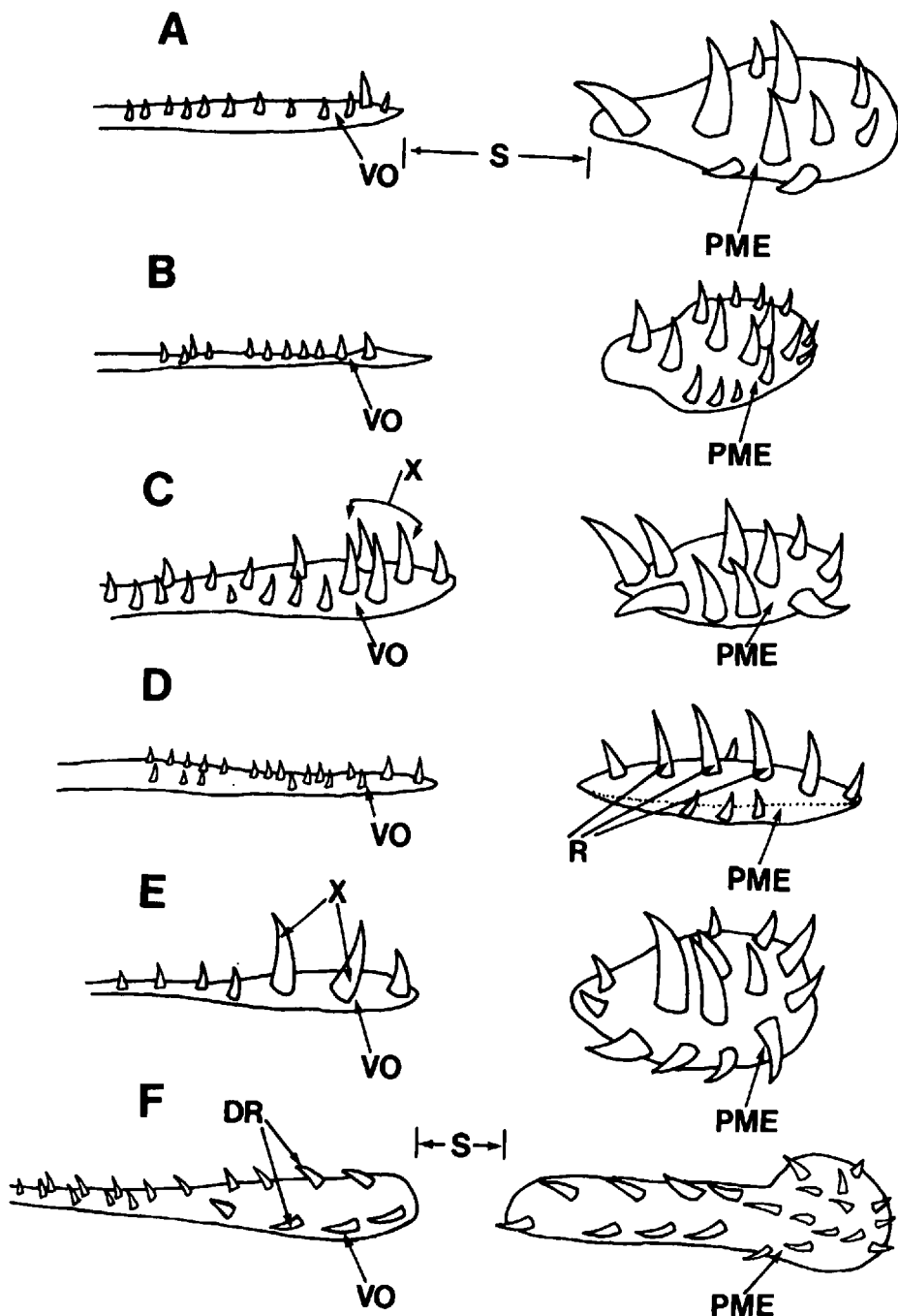


Figure 8. Dentition on the palate in: A—*Synphobranchus affinis*, ZMMU 15707; B—*S. brevitor-salis*, ZMMU 14461; C—*S. oregoni*, ZMMU 15694; D—*S. kaupii*, ZMMU 14460; E—*Diastobranchus capensis*, ZMMU 16654; F—*Histiobranchus bathybius*, IOAN uncataloged, VITIAZ Station 2220. Key: DR = double row of paired vomerine teeth; PME = premaxillary-ethmoid toothpatch; R = row of dominant median teeth on PME; S = interspace between PME and VO; VO = vomerine toothpatch; X = enlarged anterior vomerine teeth.

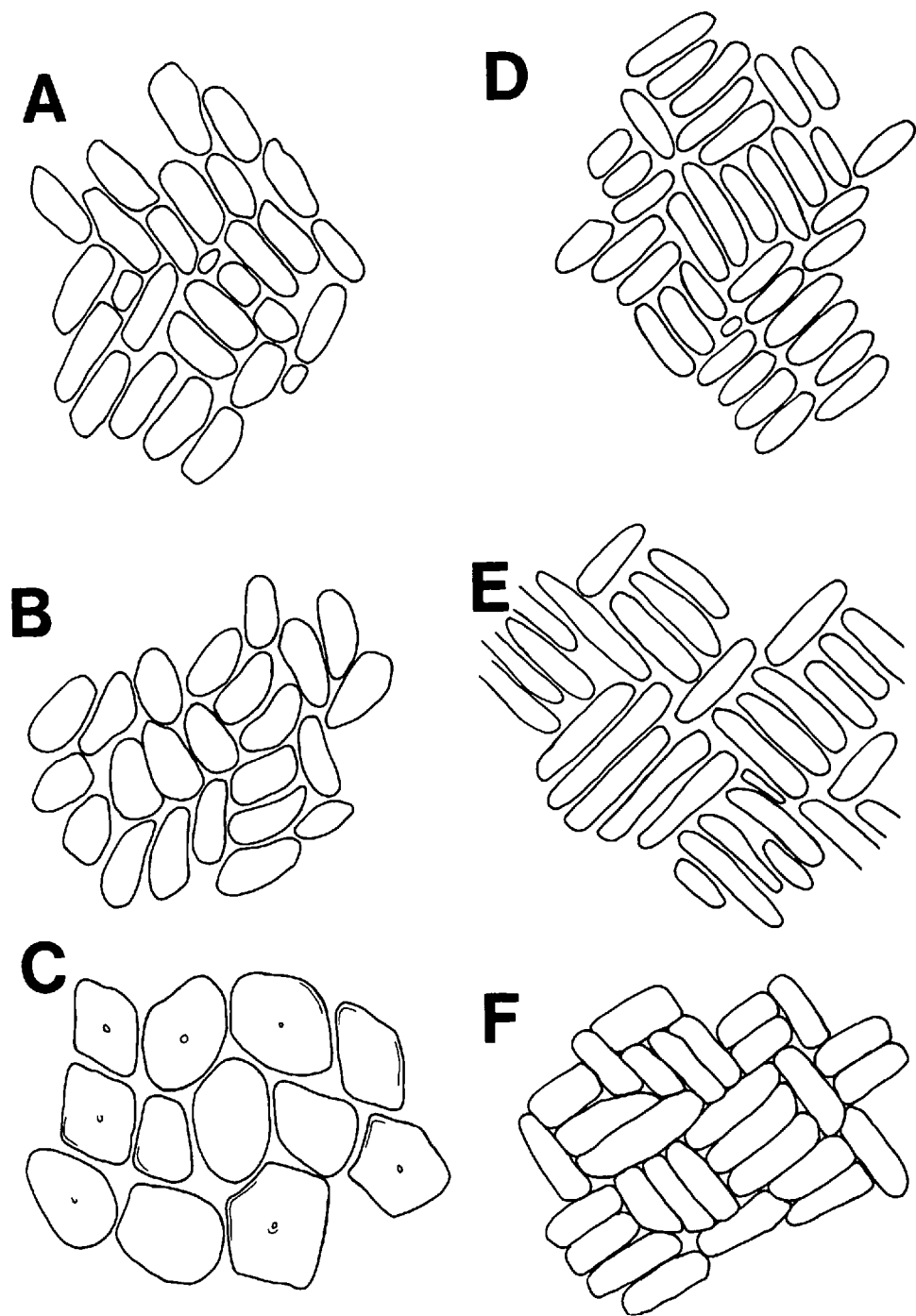


Figure 9. Scale patterns in synphobranchine genera (at a position above the lateral line, just below dorsal fin origin): A—*Synphobranchus affinis*, IOAN uncataloged, IKTIANDR Cruise 5, Station 52; B—*S. brevidorsalis*, ZMMU 14461; C—*S. oregoni*, ZMMU 15696; D—*S. kaupii*, ZMMU 14460; E—*Diastobranchius capensis*, ZMMU uncataloged, PROF. MESSIATSEV Cruise 2, Station 35; F—*Histiobranchius bathybius*, IOAN uncataloged, VITIAZ Station 2220.

- series ahead of LL (Fig. 7C), SB with one tiny pore, no STC pores; 3–4 postorbital pores in IOC; PO–LL longer than SNL; dorsal fin origin over tip of pectoral fin, far in advance of vent; anal fin origin far back, near body midpoint; PME and VO separated by a space much shorter than one-half PME length (Fig. 8F), VO without enlarged teeth anteriorly, PME club-shaped, elongate, with small teeth only, those on posterior portion in biserial array (Fig. 8F); LLA more than 40; scaled in regular, grouped, right-angle, basketweave pattern (Fig. 9F); 2–4 scales per group, length:width ratio 3:1–4:1; scales developed even in very small juveniles; gill slit horizontal, posterior end just in advance of pectoral fin base genus *Histiobranchus* 10
- 10A. LLA 44–56; TV 122–137; TL to 900 mm *Histiobranchus bathybius* Günther, 1877, bi-temperate, circumglobal, 731–4700 m.
- 10B. LLA 65–68; TV 160–164; TL to 628 mm *Histiobranchus bruuni* (Castle, 1964), abyssal basins south of Australia, New Zealand, 4198–4958 m.
- 11A. PME elongate, oval shaped, with a dominant, linear, median series of 6–8 nearly equal teeth (Fig. 8D) (lateral teeth present as well, but set low along the margins of the toothpatch and less evident); scaled in very regular, grouped, right-angle basketweave pattern (Fig. 9D); 3–6 scales per group, typical length:width ratio 3:1–4:1; dorsal fin origin relatively far behind vent—by a distance of more than one PL; musculature dense, very firm upon preservation; color gray, brown, or black with a silvery iridescent tone; VO teeth uniformly very small—the largest only as long as the smallest lateral PME tooth; LLA 27–33; TL to 905 mm; TV 141–150 *Synaphobranchus kaupii*,³ Johnson, 1862, nearly circumglobal (except eastern Pacific), 274–2869 m.
- 11B. PME short, oval or club-shaped, with irregularly placed teeth of variable size (Figs. 8A–C) 12
- 12A. Dorsal fin origin approximately opposite vent (sometimes slightly ahead or behind, but if behind vent—then never by a distance exceeding one PL); scaled in fairly regular, right-angle basketweave pattern; 2–3 scales per group, length:width ratio 2:1–3:1 (Fig. 9A); color blackish; musculature very firm; skin resilient, seldom frayed or parted around scales in preserved specimens; body slender, even in large adults; VO without enlarged teeth anteriorly (Fig. 8A)—largest tooth only subequal to smallest PME tooth; LLA 25–29; TL to 1600 mm; TV 129–150 *Synaphobranchus affinis* Günther, 1877, circumglobal, except northeastern Pacific, 290–2334 m.
- 12B. Dorsal fin origin far behind vent—at a distance typically much greater than one PL; typically scaled in irregular paving-stone pattern, neither grouped nor arranged in regular right-angle fashion; color brown; musculature flabby; skin soft, often frayed or extensively parted in preserved specimens; body bulky in large adults 13
- 13A. Scales oval or kidney-bean shaped, typically in 1:1 array, but sometimes irregularly grouped; scale length:width ratio about 2:1 (Fig. 9B); head of VO without enlarged teeth (Fig. 8B), largest VO tooth only about half the length of largest PME tooth; LLA 25–28; TL to 1110 mm; TV 131–138 *Synaphobranchus brevidorsalis* Günther, 1877, circumtropical—except northeastern Pacific, 900–3000 m.
- 13B. Scales diamond shaped, polygonal or nearly circular, arranged in highly variable paving-stone pattern (Fig. 9C); scale length:width ratio about 1.5:1–1:1; head of VO with a cluster of 3–6 enlarged teeth (Fig. 8C), largest VO tooth about equal in length to largest PME tooth; LLA 27–34; TL to 1110 mm; TV 127–148 *Synaphobranchus oregoni* Castle, 1960, nearly circumtropical—except eastern Pacific, 512–1900 m.

New Species Descriptions

Ilyophis robinsae new species

Figs. 3C, 4B

Material (one specimen).—Holotype: ZMMU P14759, 348 mm TL, VITIAZ Cruise 57, Station 7237, 28 II 1975, 07°39.9'N, 121°32'E, 4800 m depth.

Diagnosis.—Refer to key above.

Description.—MERISTICS: TV 141, LLA 32/33 (L/R), LLT 90/87. MORPHOMETRICS in percent TL: HL 10.7, PD 15.1, PA 31.6; in percent HL: SNL 37.5, ED

³ Spelling of the species name as per original orthography is "kaupii" (Johnson, 1862); the subsequent spelling "kaupi" constitutes an incorrect emendation (Ride et al., 1985).

8.3, PL 13.6, LGA 12.8. OTHER CHARACTERS: Head without prominent parietal-occipital swelling, tapering rapidly from nape to low slender, conical snout (Fig. 3C); toothed upper jaw extending only slightly beyond lower; fleshy snout tip projecting beyond tip of lower jaw; snout tip with few simple plicae; posterior nostril as simple aperture, no flap, marginal papillae very small and inconspicuous; PME teeth small and numerous, with six posterior teeth somewhat enlarged; outer PME teeth about equal in size and shape to dentary teeth, VO with single median row of enlarged teeth (Fig. 4B); pectoral fin small, narrow, its length just exceeding gill slit length (Fig. 3C); gill slit nearly horizontal; dorsal fin origin just behind tip of appressed pectoral fin (by one-half PL); anus located one third TL from snout tip; body very slender, greatest depth 4.3% TL; body naked; lateral-line pores indistinct against general body color of translucent grey; lateral-line tubule ending at circa 74% TL (body is abraded; tubule may extend further back in life); SOC with only three pores (four on right side in holotype), confined to snout region; no pores in SB, TS or STC (Fig. 3C).

Comparative Remarks.—Although described from just a single specimen, the new abyssal species *I. robinsae* is unquestionably distinct. The naked condition may represent a juvenile character state since the holotype is of moderate length. However, most scaled synphobranchid species have a full scale complement by TL 300 mm. The highly variable nature of squamation in the congener *I. arx* prompts caution in definitive diagnosis of this character when only one specimen is available for study. Among members of the genus, *I. robinsae* is most similar to *I. brunneus*. These two species, together with *I. arx*, display a similar pattern of reduction in pores of the cephalic lateralis system. All three also lack a flap on the posterior nostril. We tentatively assign these species to a subgeneric species group termed the “*brunneus*” group. The two species *I. robinsae* and *I. brunneus* differ most notably in number of PME teeth (ca 52 versus 21, respectively, Fig. 4B cf 4A) and squamation (naked versus fully scaled).

Distribution.—Refer to zoogeography section below.

Etymology.—Named for Catherine H. Robins in recognition of her substantial contributions to knowledge of synphobranchid eels.

***Ilyophis nigeli* new species Shcherbachev and Sulak**
Figures 1C, 2B, 4C

Material (nine specimens).—Holotype: ZIL 45274, 513 mm TL, mature female with ca 1.0 mm ova, GERAHL Trawl 66, 10 II 1979, 42°27'N, 144°27'E, 1160 m depth. Paratypes (eight): USNM 339093 (former ZIL 42575), 410 mm TL, GERAHL Trawl 135, 6 II 1979, 37°43'N, 142°35'E, 1540 m depth; ZIL 45767, 403 mm TL, MIS DALNIY Trawl 18, 30 I 1981, 37°43'N, 142°18'W, 750 m depth; ZIL 48481, 363 mm TL, EKVATOR Trawl 166, 31 XII 1972, 44°07'N, 146°34'E, 1020 m depth; ZIL 48482, 2 specimens—320–345 mm TL, EKVATOR Trawl 206, 8 I 1973, 42°21'N, 143°55'E, 700 m depth; ZIL 48483, 406 mm TL, PROFESSOR Trawl 97, 44°21'N, 148°40'E, 1200 m depth; ZIL 49224, 373 mm TL, SHANTAR Trawl 116, 23 IV 1975, 35°20'N, 144°22'E, 1780 m depth; ZMMU 17952, 406 mm TL, VITIAZ Station 2078, 11 V 1953, 44°09'N, 148°39'E, 1170 m depth.

Diagnosis.—Refer to diagnostic key above.

Description.—Data presented are for holotype with range for paratypes given in parentheses. MERISTICS: TV 141 (141–146), LLA 36 (32–39), LLT 96/95 (left/right) 88–101. MORPHOMETRICS in percent TL: HL 11.0 (10.7–12.4), PD 13.6 (13.1–15.5), PA 30.3 (28.2–32.7); in percent HL: SNL 26.7 (25.7–33.8), ED 11.7 (10.3–12.1), PL 18.0 (16.4–20.4), LGA 13.7 (10.5–15.6). OTHER CHARACTERS: Head without prominent parietal-occipital swelling, tapering gradually to some-

what inflated snout (Fig. 1C); toothed upper jaw extending beyond lower; fleshy snout tip projecting beyond tip of lower jaw, with several well-developed plicae; posterior nostril with lunate flap, flap and nostril rim ornamented with small papillae only (Fig. 2B); gill slits horizontal to slightly oblique; completely scaled, except almost entirely naked on abdomen below lateral line; scales set in irregular right-angle basketweave pattern; 1–6 long scales per group; scales embedded, often indistinct, highly variable in length; PME and VO nearly in contact, teeth on each bone of irregular size and placement (Fig. 4C); pectoral fin small but relatively broad-based, PL noticeably exceeding gill slit length; gill slit slightly oblique; dorsal fin origin just behind tip of appressed pectoral fin (by approximately one PL); anus located one-third TL from snout tip; body slender, greatest depth 5.3% TL; lateral-line pores white, distinct against general body color (grey-brown in preservation) anteriorly; lateral-line tubule (including pores) ending at 67–73% TL; SOC with six pores (fourth pore absent in ZIL 45767 paratype, Fig. 1C); one pore in SB; one STC pore (absent in ZIL 45767); no TS pores.

Comparative Remarks.—The new species has a full complement of six prominent pores in the SOC series (Fig. 1C). In the study series there is always at least one pore in the STC canal. The aperture of the posterior nostril is partially occluded by a prominent flap (Fig. 2B). In these three regards the condition in *I. nigeli* matches that of *I. blachei* (Figs. 1B, 2A). The remaining members of the genus have only three SOC pores, lacking pores above the eye. Moreover, they also lack a flap on the posterior nostril, again appearing to substantiate a distinct sub-generic species group, which we term the “*blachei*” group. However, such a grouping of convenience remains to be substantiated systematically. Reduction in size and number of cephalic lateralis pores is a common theme within all synphobanchid taxa, a character condition to be viewed with caution. Furthermore, presence or absence of a nostril flap is another feature with an apparent mosaic distribution within the family (Fig. 2). Thus, in addition to development in species of the “*blachei*” group, a flap is also present, for example, in *D. capensis* (Fig. 2C) and *S. kaupii* (Fig. 2E). Similarly, in parallel to members of the “*brunneus*” species group, a flap is absent in *H. taxis* (Fig. 2D) and *S. brevidorsalis*.

Distribution.—Refer to zoogeography section below.

Etymology.—Named for Nigel R. Merrett in recognition of his substantial contributions to knowledge of genus *Ilyophis* and other synphobanchid eels.

Systematics and Taxonomy

Except for Castle's (1964) early summary, previous systematic treatments of synphobanchid eels have been limited to a particular taxonomic group and/or geographic region (Robins 1971—Straits of Florida; Robins and Robins 1989—western North Atlantic; Karrer 1982—Mozambique Channel; Saldanha and Merrett 1982, Merrett and Saldanha 1985—eastern North Atlantic). However, the distributions of most species span more than one ocean. Furthermore, characters (including vertebral count and coloration) undergo some regional intraspecific variation. Thus, there is a need to consider character variation across the entire species range, both in diagnosing and distinguishing species.

The synphobanchid eels are morphologically specialized in the fashion typical of all eels, i.e., highly modified for a life history originally involving burrowing and exaggerated anguilliform locomotion (e.g., long flexible skeleton and slender body, reduced and fused head bones, expanded gill chambers with restricted openings, reduced paired fins and squamation). Anguilliform functional convergence,

resulting in a very limited suite of phylogenetically useful characters, presents an obstacle to the study of the systematics of all families of eels. Furthermore, within the Synphobranchidae, parallel anguilliform adaptations are evident among the subfamilies and genera in terms of further reduction, loss and fusion. These are variably expressed in individual species, resulting in a mosaic of states that defy ready use in taxonomic diagnoses. Thus, the utility of many species-level characters in assessing and diagramming higher relationships is limited. Previous "diagnoses" of genera and subfamilies have tended to be descriptively comprehensive, but equivocal in terms of diagnostic definitions of taxa. Moreover, there has been little attempt to assess the direction of specialization (polarization of character transformation) in the family by comparative reference to less specialized outgroups (e.g., Anguillidae, Congridae, other Elopomorpha, Halecomorpha). Thus, shared primitive characters have not been eliminated from among those typically used to define taxa.

Status of Subfamilies.—Due to considerable redundancy and parallelism, it remains difficult to unequivocally define and differentiate the subfamilies Synphobranchinae and Ilyophinae (Robins and Robins, 1976; Saldanha and Merrett, 1982, 1987; Merrett and Saldanha, 1985). This has previously been acknowledged in the naming of *H. texis* (Robins and Martin, in Robins and Robins, 1976), a species allocated to the Synphobranchinae, but rather uncomfortably so (i.e., numerous ilyophine-like exceptions in couplet 2A of the key above).

All three subfamilies are specialized in divergent directions in terms of jaw plus cranium form and function. However, each subfamily retains certain primitive features (Robins and Robins, 1989), variously expressed in one or more species. There is also considerable parallelism among the subfamilies with respect to trends in reduction and loss. It is very difficult to determine which subfamily is the least specialized (i.e., most primitive taxon) overall. The statement that the Simenchelyinae represents the most primitive lineage (Robins and Robins, 1989) is unverifiable. Direction of character transformation has yet to be established by appropriate outgroup comparison.

SUBFAMILY SIMENCHELYINAE AND GENUS *SIMENCHELYS*. This monotypic subfamily/genus is highly distinctive due to specialized food habits. It is noteworthy, however, that despite specialization of the mouth and jaws, *Simenchelys* displays a primitive condition with respect to certain characters. For example, the body is completely scaled. The hyomandibula is distinctly canted anteriorly, a condition also seen in *I. blachei*. The hyomandibula-quadrato complex in *Simenchelys* is stated to be vertically aligned (Robins and Robins, 1989, p 214) or inclined slightly forward (Robins and Robins, 1976, p 277). But, radiographs of our study specimens display a distinctly anteriorly canted hyomandibula (acute angle between hyomandibular ridge and long axis of parasphenoid), which agrees with Jacquet's dissection (1920, plate I, fig. 11; plate II, fig. 38). Robins and Robins (1989) contend that the strongly posteriorly canted hyomandibula of synphobranchines is the primitive condition for the family. However, outgroup comparison with the basal anguilliform fishes *Anguilla* (Smith, 1989a, fig. 6) and *Conger* (Smith, 1989b, fig. 509g), the elopomorph teleosts *Elops* (Ridewood, 1904) and *Megalops* (Gregory, 1933, fig. 31), and the halecomorph *Amia* (Allis, 1888), establishes that an anterior cant corresponds with the primitive and general condition of the suspensorium in neopterygian fishes, including basal eel families. A backwardly canted hyomandibula is a very unusual feature, being limited to a few highly specialized teleosts having capacious gapes including all ipnopsine chlorophthalmids, a few synodontids (Sulak, 1977a), and the Giganturidae (Rosen,

1973). Among anguilliform fishes, aside from the Synphobranchidae, a somewhat backward canted hyomandibula occurs only in the Muraenidae (Böhlke et al., 1989, fig. 112); among other elopomorph fishes, only in the very aberrant Saccopharyngiformes (Robins and Robins, 1989).

It seems probable that the backward canted hyomandibula in the Synphobranchinae is an adaptation directed toward jaw mobility and flexibility in handling of large active nektonic prey. The overall jaw configuration probably results in a relative reduction in bite power (although the well-muscled jaws of the Muraenidae and *Dysomma* provide contrasting adaptive end-points accompanying a backward canted hyomandibula). The condition of the jaw suspension in the most ilyophines (vertical hyomandibula) represents the more generalized one, enabling handling of a relatively broad size spectrum of prey in the elongate mouth, with limited sacrifice in bite power. However, comparative configuration and development of jaw musculature within synphobranchid eels have not been studied. Even among related taxa, a backwardly canted suspensorium can be provided with very different configurations of adductor mandibulae (compare *Saurida* and *Harpadon* in Rosen, 1973, figs. 38 and 39, with *Ipnops*, fig. 28). A comparison of jaw musculature in *Synphobranchus* (light cranium, weak dentition) versus *Dysomma* (heavy cranium, powerful dentition), both with a posteriorly inclined suspensorium, would be valuable. The ultimate synphobranchine development of an elongate, backward canted jaw suspension, coupled with an up-curved, projecting lower jaw, occurs in *D. capensis* (Castle, 1975, fig. 1). This species attains the largest size of any synphobranchid eel and probably captures rather large swimming prey. The unusually long and uniquely falciform pectoral fins of this species apparently correspond with greater maneuverability as compared to other synphobranchids. The strongly anteriorly canted hyomandibula of the small-mouthed *Simenchelys* vis-à-vis that of the synphobranchines represents an alternative jaw specialization apparently directed toward powerful flesh tearing and mastication (Robins and Robins, 1989). The blunt, stout, well-muscled head of *Simenchelys* conforms well with such an ability, and contrasts with the slender, conical head of other synphobranchids.

That the jaw configuration in the Synphobranchinae is adaptive rather than primitive tends to be substantiated by the highly derived condition of the pterygoid in *Synphobranchus*, versus the less derived condition in *Simenchelys* and *Ilyophis*. This bone in *Synphobranchus* has become obsolete in accompaniment with rearward elongation of the jaw mechanism via strong backward canting of the hyomandibula. Parallelism in jaw modification is displayed in the Ilyophinae where strong backward canting of the hyomandibula in the highly derived genus *Dysomma* (Robins and Robins, 1976) is again accompanied by loss of the pterygoid. This condition contrasts with the anteriorly canted or vertical hyomandibula and fairly well-developed pterygoid in the relatively conservative ilyophine species *Ilyophis blachei* (Saldanha and Merrett, 1987) and *Atractodenchelys phrix* (Robins and Robins, 1970). Interpreting polarity in this character is important since a strongly posteriorly canted hyomandibula is the only derived character shared by all synphobranchine genera.

Simenchelys displays a derived condition with respect to reduction of cephalic lateralis pores (Fig. 1A). The SOC series is reduced to the three anteriormost pores, the IOC series to five pores, the hyomandibular series to six pores. The SB and STC canal are absent. Parallel trends in head pore reduction result in a comparable condition in each of the other two synphobranchid subfamilies (*I. robinsae* and *H. texis*, figs. 3C and 7A, respectively). A complete canal system

with a full complement of pores must be considered the primitive condition for the family.

SUBFAMILY ILYOPHINAE. Together, the premaxilla-ethmoid + parasphenoid + basisphenoid bones form a thick, heavy median cranial keel. This keel strengthens the snout region, supporting the relatively broad grasping/grinding tooth pads of an upper jaw and palate adapted to process benthic invertebrates. In conjunction with development of this strengthened median keel the bony eye socket is restricted (Robins and Robins, 1989). Correspondingly, the eyes are relatively reduced in size (least so in the conservative species *I. blachei* and *A. phrix*), while the olfactory apparatus is lengthened and enlarged. The linear (versus upturned) profile of the gape may reflect facilitation of lateral side-to-side grinding of the jaws. These characteristic specializations are put into comparative context below.

SUBFAMILY SYNAPHOBRANCHINAE. The projecting and upturned lower jaw plus strongly posteriorly canted suspensorium suffice to define the subfamily Synaphobranchinae and distinguish it from the Ilyophinae (in particular the genera treated herein). The long, lightly-built lower jaw, small jaw teeth, and backward canting hyomandibula together achieve an elongate, capacious, weakly-toothed buccal cavity. The main structural theme of osteological lightness and elongation of the gape in the subfamily is matched by the correspondingly delicate architecture of the median cranial keel—the conjunction of premaxilla-ethmoid + parasphenoid + basisphenoid + vomer (Castle, 1975, fig. 1A; Robins, 1971, figs. 2–4; Robins and Robins, 1976, fig. 7A). Laterally, the pterygoid arc is similarly reduced to either a detached “floating” vestige as in *Synaphobranchus* and *Haptenchelys* (Robins and Robins, 1976) or reduced to a slender rod as in *Diastobranchus* (Castle, 1975). This reductional theme coordinates with greater vertical and fore-and-aft jaw mobility in synaphobranchines.

Some characters previously included in subfamily-level diagnoses of the Synaphobranchinae vis-à-vis Ilyophinae (including former Dysommidae) vary widely and in parallel within both taxa, and are consequently of little taxonomic utility above the species or generic levels. Included here are the following: inclination of the gill slits (horizontal vs oblique), condition of the pterygoid, extent and type of squamation (scaled vs naked; basketweave vs paving stone), and reduction or loss of pores in the supraorbital canal, supraorbital branch, and supratemporal commissure canal.

Status of Genera.—**GENUS SYNAPHOBRANCHUS.** As understood herein, this genus comprises a well-defined group of four very similar species readily diagnosed by the confluent, ventrally-placed gill slits—in addition to other characters given in the key above or discussed comparatively under *Diastobranchus* and *Histiobranchus* below. Robins and Robins (1989) include species of *Diastobranchus* and *Histiobranchus* within *Synaphobranchus*, resulting in a heterogeneous assemblage that defies ready diagnosis.

GENUS HISTIOBRANCHUS. *Histiobranchus* was originally erected by Gill (1883) to distinguish *S. bathybius* Günther 1877 from other species attributed to that genus. Subsequently Regan (1913) and others (Castle, 1960) treated *Histiobranchus* as a subgenus of *Synaphobranchus*. However, in describing a second species of *Histiobranchus*, Castle (1964) argued for resurrection of the genus, citing characters that unite *H. bathybius* and *H. bruuni* (notably, separate gill slits, far anteriorly placed dorsal fin, and very long abdomen), and which distinguish these species from *Synaphobranchus* (gill slits confluent along the ventral midline, dorsal fin origin near or behind anus, anus located within anterior 16% of TL). The last two characters also distinguish *Histiobranchus* from *Diastobranchus*. Sub-

sequent authors, however, have continued to recognize *Histiobranchus* only at the subgenus level. Most recently Robins and Robins (1989) have again placed *Histiobranchus* in synonymy with *Synaphobranchus*. They argue that the two species of *Histiobranchus* are united only by shared primitive characters. However, some important shared characters of a clearly derived nature were not considered by Robins and Robins (1989).

In addition to the important differences between *Histiobranchus* and *Synaphobranchus* (sensu stricto) noted by Castle (1964), four other differences are significant. First, species of *Histiobranchus* are unique among all synaphobranchines in having a peculiar, elongate club-shaped premaxillary-ethmoid toothplate (Fig. 8F) (versus relatively much shorter and oval shaped in *Synaphobranchus*, Figs. 8A–D). In contrast to *Synaphobranchus*, this toothplate is set very close to the vomerine toothplate and provided with unusual dentition. In *Histiobranchus* the teeth on the elongate shaft of the PME as well as those on the adjoining VO are typically arrayed biserially in parallel rows (Fig. 8F) as has previously been illustrated (Bruun, 1937, fig. 1A). The depiction of palate dentition in Robins and Robins (1989, fig. 219) is inaccurate. In all other synaphobranchines the PME teeth are either randomly placed (Figs. 8A–C, E) or in *S. kaupii* (Fig. 8D) arrayed marginally around a dominant median row (as accurately figured in Bruun, 1937, fig. 1B). Secondly, the pectoral fin in *Histiobranchus* is very short, tapering symmetrically to a rounded tip (versus long and tapering asymmetrically to a fine pointed tip distally in *Synaphobranchus*, as well as in *Diastobranchus*). When pressed anteriorly against the body the pectoral fin in *Synaphobranchus* reaches to or nearly to the posterior corner of the gape; it falls well short of this point in *Histiobranchus* (Fig. 3C). Thirdly, the temporal portion of the cephalic lateralis canal in *Histiobranchus* is well-developed and characteristically perforated by three pores, grouped ahead of the supratemporal cross commissure canal and distinct from the lateral line proper (Fig. 7C). Castle (1964) correctly identified these pores as distinct from the lateral line in his discussion, and as illustrated in his figures 1B and 1E. Not only is the temporal canal in *Histiobranchus* elongated, but so is the entire occipital (post-orbital) portion of the head, with accompanying rearward displacement of the lateral-line canal and rearward elongation of the jaw. Correspondingly, post-orbital distance to the first lateral-line pore substantially exceeds snout length in *Histiobranchus* (Fig. 7C) as opposed to falling well short of snout length in *Synaphobranchus* (Figs. 5, 6) and *Diastobranchus* (Fig. 7B). Similarly, post-orbital distance to the posterior corner of the gape equals twice the horizontal eye diameter in *Histiobranchus* (Fig. 7C), versus only half that in *Synaphobranchus* (Figs. 5, 6) and *Diastobranchus* (Fig. 7B). Fourthly, the four species of *Synaphobranchus* have a low and similar number of lateral-line pores to the level of the vent (25–31 in *S. affinis*, 25–28 in *S. brevidorsalis*, 27–33 in *S. kaupii*, 27–34 in *S. oregoni*). The count in *D. capensis* is similar (22–27). By contrast, the two species of *Histiobranchus* display counts considerably outside of the *Synaphobranchus* range of 25–34 (i.e., 44–56 in *H. bathybius*, 65–68 in *H. bruuni*). The two species of *Histiobranchus* clearly differ as substantially from the four species of *Synaphobranchus* as does the genus *Haptenchelys*, and therefore warrant distinction at the equivalent generic level.

It could be argued that the elongate perforated temporal canal in *Histiobranchus* is not a novel specialization, but a primitive retention. It may be assumed that a full complement of major and minor cephalic lateralis pores was present in elopomorph ancestors, using the halecomorph pre-teleost *Amia* (Allis, 1888) for out-group comparison. Closer to the Anguilliformes, evidence of direction of specialization is equivocal. Within the anguilliform sister-group, Notacanthiformes,

the eel-like notacanthus have a short temporal canal with 1–2 pores. Among presumptive basal Anguilliformes, *Anguilla* and *Conger* lack pores in the temporal canal (Smith 1989a, 1989b). There is a trend in the Synphobranchidae for reduction and loss of cephalic pores independently within each subfamily and most genera. Overall, *Histiobranchus* represents no exception in this regard. Pores in the infraorbital canal are minute; those in the preopercular-mandibular canal reduced in number; those in the supratemporal cross-commissure and the supraorbital branch (Fig. 7C) minute or absent. Thus, the unique occurrence of three temporal canal pores, together with unique elongation of the occipital portion of the body in *Histiobranchus* is interpreted herein as a genuine novelty that counters the broad reductive trend in the cephalic lateralis system within the Synphobranchidae, and sets *Histiobranchus* apart from other genera in the family.

GENUS *DIASTOBRANCHUS*. Except for the very singular *Simenchelys*, *Diastobranchus* is alone among all other synphobranchids in possessing a pterygoid bone articulating with both the quadrate posteriorly and the premaxillary-ethmoid anteriorly (Castle, 1975). This condition must be interpreted as retention of a primitive feature. It contrasts with that in both the more specialized synphobranchine species and ilyophine species. The former have a vestigial “floating” pterygoid as illustrated by *Synphobranchus* and *Haptenchelys* (Robins, 1971; Robins and Robins, 1976). The latter have the pterygoid reduced from its anterior end to a slender remnant attached only to the quadrate (Robins, 1971; Merrett and Sandanha, 1985). Thus, there are at least four conditions regarding pterygoid specialization within the family as respectively exemplified by *Diastobranchus*, other Synphobranchinae, the Ilyophinae (excluding *I. blachei*) and *Simenchelys*. The condition of the pterygoid in *Diastobranchus* suggests this genus has differentiated at a lower level of generality than the four members of the genus *Synphobranchus*, and thus does not belong within that genus. *Diastobranchus* bears a superficially similarity to *S. kaupii* in shared primitive characters, including complete grouped basketweave squamation.

As figured by Castle (1975), other disparities in cranial features appear to distinguish *Diastobranchus* from *Synphobranchus*, including comparative development of the preopercle, interopercle, and hyomandibular-sphenoid junction. Such apparent differences bear further comparative osteological investigation.

The widely and distinctly separate gill slits of *Diastobranchus* offer a second morphological counterpoint with respect to *Synphobranchus*. Again the *Diastobranchus* condition must be considered a primitive retention, in parallel to *Histiobranchus* and *Haptenchelys*. Tightly confluent gill slits are displayed only in *Synphobranchus*, and represent a unique derived condition peculiar to that genus.

A third point of taxonomic differentiation concerns median fin placement. Despite some species-level differences in dorsal and anal fin origins, the four species of *Synphobranchus* are closely similar in having the dorsal origin approximately opposite or behind that of the anal fin. Along with *Histiobranchus* and *Haptenchelys*, however, *Diastobranchus* differs markedly from *Synphobranchus* in vertical fin placement. Robins and Robins (1989) downplay such differences, suggesting median fin placement may be “non-adaptive” in synphobranchids, leading to species differences in fin position. This seems extremely improbable for the synphobranchines which are highly adapted to life as swimming predators of active prey. Both median fin form and placement are important in achieving optimum body surface area for greatest possible thrust, braking and turning in anguilliform locomotion (Gosline, 1968; Alexander, 1974). Underwater photographs of large *Histiobranchus* (B. Hecker, pers. comm.) confirm that the median fins in this genus are not collapsed during swimming, but are kept fully raised

during normal locomotion. The same is undoubtedly true with respect to *Diastobranchus*, functionally equivalent to *Histiobranchus* as a large, active nektonic predator on large mobile prey. Thus, the long, high dorsal fin of *Histiobranchus* cannot be deemed non-adaptive.

The polarity of specialization in median fin origin is equivocal. However, a dorsal fin origin over the pectoral fin and gill slit, but far in advance of the vent, is the widespread condition among anguilliform families. *Anguilla* represents a notable exception, as do the four species of *Synaphobranchus* among the Synphobranchidae, all of which have a dorsal origin close to the anus and far behind the head. Overall, a far anterior origin of the dorsal fin seems the probable primitive and general condition in eels. The abbreviated *Synaphobranchus* dorsal fin seems the probable derived condition, representing a significant point of differentiation from *Diastobranchus* and other synphobranchid genera with long dorsal fins originating just behind the head.

GENUS *HAPTENCHELYS*. As correctly determined by Robins and Robins (1976), but not specified in their generic diagnosis, the elongate, backwardly canted hyomandibula of *Haptenchelys* aligns it with the subfamily Synphobranchinae. Unlike other synphobranchines, however, *Haptenchelys* converges closely upon the general *Ilyophis* plan, suggesting a similar bottom-hugging (vs. nektonic, benthopelagic) life style. The elongate head, slender snout, and linear gape resemble those of *Ilyophis*. In contrast to other synphobranchines, the PME and VO in *Haptenchelys* are nearly contiguous (i.e., not distinctly separated), and the VO bears a median row of enlarged teeth as in *Ilyophis*. In converging on a stouter *Ilyophis*-like cranial plan, *Haptenchelys* departs somewhat from the synphobranchine structural theme. Correspondingly, as the palate has been strengthened to support stronger vomerine dentition, the orbit has been accordingly constricting. Other *Ilyophis*-like similarities include reduction in PL, reduction in number of cephalic lateralis pores (Fig. 7A), far anterior origin of the dorsal fin, loss of scales, and presence of simple plicae on the tip of the snout.

Robins and Robins (1976) state that *Haptenchelys* might best be likened to a naked *Diastobranchus* based on external characters. However, the analogy is rather imprecise. In many respects *Diastobranchus* represents the apex of synphobranchine osteological trends in cranial structure in coordination with the grasping plus swallowing whole of large nekton prey. Other morphological features, including large body size, long falcate pectoral fins, and large eyes, coordinate with active benthopelagic foraging mediated by vision and the lateral-line sense. On the other hand, *Haptenchelys* departs from these trends, morphologically and probably behaviorally, mimicking *Ilyophis* as a benthic olfactory forager on smaller benthic prey. Prey handling in the latter two genera probably involves oral mastication of benthic invertebrates prior to swallowing. *Diastobranchus* has a very large eye with a correspondingly very large orbital opening; *Haptenchelys* has a reduced eye within in a restricted orbit. In contrast to the exceptionally well developed pectoral fin in *Diastobranchus*, *Haptenchelys* has a very small, weak pectoral fin. *Diastobranchus* has a foreshortened snout with a distinctly projecting lower jaw; *Haptenchelys* has an elongate snout with jaws of equal length.

The slender, elongate, backwardly canted hyomandibula of *Haptenchelys* is typical of the subfamily Synphobranchinae. A backwardly canted, but stouter, hyomandibula also occurs independently in advanced ilyophine genera as exemplified by *Dysomma* (Robins and Robins, 1976, fig. 7C). In synphobranchines there is an expansive interorbital opening between the premaxilla-ethmoid and the basisphenoid, bridged ventrally by a slender parasphenoid and weak vomer. In ilyophines the interorbital space is greatly constricted by strengthening and

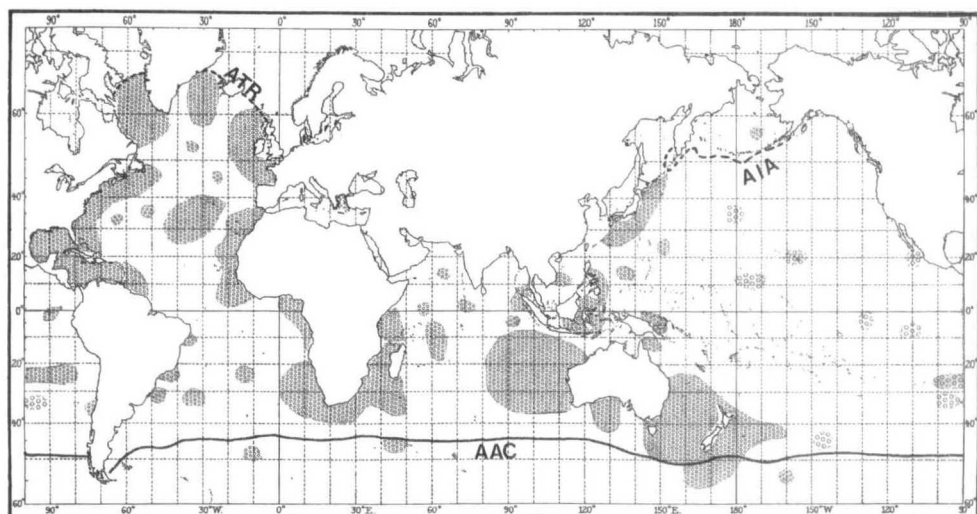


Figure 10. Distribution of family Synphobranchidae (shaded areas) based on known records of the six genera treated herein. Key: AAC = Antarctic Convergence, AIA = Aleutian Island Arc, ATR = Arctic Transversal Ridge.

thickening of the same bones, as illustrated in *I. arx* (Robins and Robins, 1976, fig. 7B). Strengthening of the cranial keel corresponds with the presence of large, strong teeth borne on the underlying vomer, a characteristic feature of ilyophines, culminating in the enlarged teeth of *Dysommia* and *Dysomma* (Robins and Robins, 1976, figs. 6, 7). Reduction in orbital dimensions in ilyophines accompanies restriction of the interorbital opening in association with strengthening of the anterior portion of the skull. Reduction in relative size and apparent importance of the eyes as sense organs of distant perception is offset by increased development of the olfactory apparatus, suggesting a general dichotomy in comparative life history strategies of ilyophine versus synphobranchine deep-sea eels.

The impression of similarity between *Haptenchelys* and *Ilyophis* is reinforced by the lack of scales, and presence of plicae on the tip of the snout (Merrett and Saldanha, 1985, fig. 4). The condition of the toothed tip of the lower jaw in *Haptenchelys* is intermediate between the condition generally typical of either subfamily. It does not project ahead of the toothed tip of the upper jaw as in other synphobranchines, nor does the toothed tip of the upper jaw project beyond that of the lower as in ilyophines (Robins and Robins, 1976, fig. 7A.). The condition of the premaxilla-ethmoid block and the parasphenoid keel is also somewhat intermediate, but in association with enlarged vomerine teeth, more closely approximates that of *Ilyophis* than *Synphobranchus*. In view of the canted hyomandibula, such features are interpreted as convergence by *Haptenchelys* on the *Ilyophis* plan.

Zoogeography

The global distribution of the six genera treated herein is shown in Figure 10 based on records we accept as valid. The combined distributions of these genera essentially define the pattern for the family Synphobranchidae as a whole, a pattern which would not be substantially altered by addition of the few available records of genera (*Atractodenchelys*, *Dysomma*, *Dysommia*, *Meadia*, and *Thermobiotus*) excluded from the present study. The family is basically circumglobal

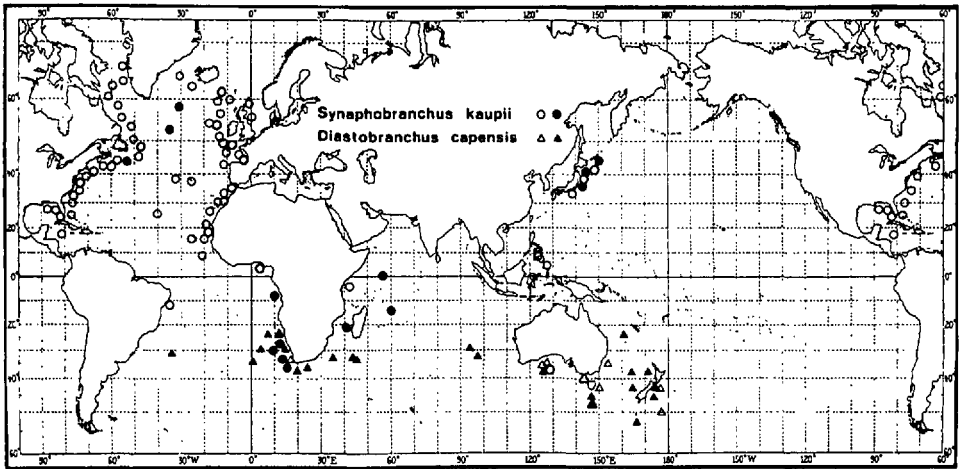


Figure 11. Distribution of *Synphobranchus kaupii* and *Diastobranchus capensis*. Solid symbols = Russian records; open symbols = other records.

with near absence from polar watermasses, and very sparse representation in the northeastern Pacific. However, deep-sea sampling effort has been very unevenly distributed, with heaviest concentration in the North Atlantic. The family is undoubtedly more continuously and equitably distributed than Figure 10 indicates. The picture of global synphobranchid distribution has been substantially supplemented by Russian investigations in the Southern Hemisphere over recent decades. Approximate latitudinal limits in the Northern Hemisphere are the Arctic Transversal Ridge in the Atlantic and the Aleutian Island Arc in the Pacific. Arctic records are limited to a single Russian capture of *S. affinis* from the "Bering Sea" (ZIL 37518, without precise locality data) and a single "USS Albatross" capture of *H. bathybius* (USNM 48693, Gilbert, 1896). Latitudinal limits in the Southern Hemisphere coincide closely with the Antarctic Convergence except for a few captures of *D. capensis*, *H. bathybius* and *H. bruuni* (Castle, 1968) (Figs. 11, 12) from marginal Southern Ocean waters, primarily on the slopes of major seamounts and in deep basins off Australia/New Zealand enclosed to the south by the Southeast Indian Ocean Ridge (known to Russian oceanographers as the Australo-Antarctic Rise) and the Pacific Antarctic Ridge (known as the South Pacific Ocean Rise).

As yet the demersal deep-sea fish fauna of the southwestern Pacific remains very poorly explored. However, new Russian records from that and other regions are sufficient to define a family distribution that conforms closely with a prevailing pattern among numerous and diverse taxa of deep-dwelling demersal fishes. This pattern is one of broad circumglobal occurrence in tropical and temperate watermasses, but absence from or rarity in the northeastern Pacific (Fig. 10).

The demersal deep-sea fish fauna of the northeastern Pacific is notable vis-à-vis the fauna of the rest of the tropical-temperate world ocean in lacking a number of dominant or otherwise ubiquitous taxa. The Synphobranchidae is one of those taxa. Sampling artifact cannot be invoked to explain the virtual absence of synphobranchids (except for one record each of *S. affinis* and *H. bathybius* from the Bering Sea, and one record of *H. bathybius* off the tip of Baja California) from the northeastern Pacific, at least one portion of which has been the object of an intensive deep bottom trawling study (Pearcy et al., 1982). Moreover, a distri-

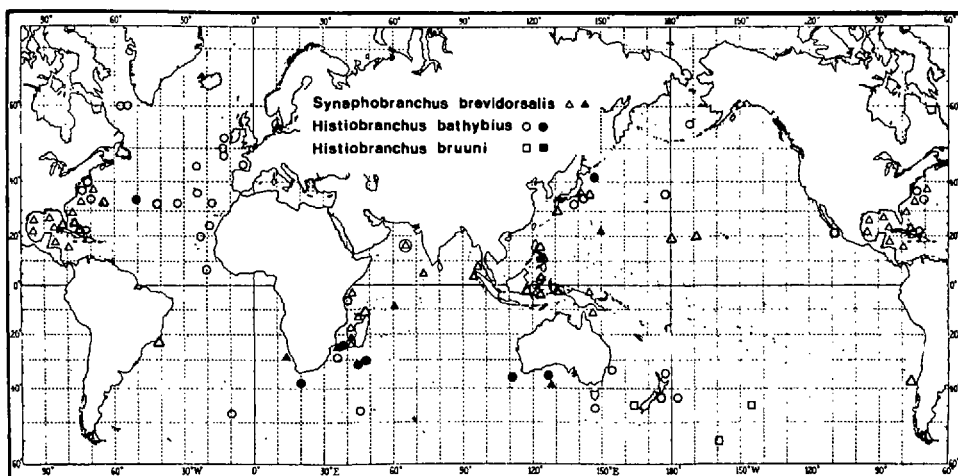


Figure 12. Distribution of *Synphobranchius brevidorsalis*, *Histiobranchius bathybius*, and *H. bruuni*. Solid symbols = Russian records; open symbols = other records; encircled symbol = record with approximate locality data only.

bution nearly identical to that of the Synphobranchidae is displayed, for example, by the aulopiform genera *Bathysaurus* (Sulak et al., 1985) and *Bathypterois* (Sulak, 1977a). The general absence from the northeastern Pacific of the Synphobranchidae and other dominant demersal deep-sea fish taxa is difficult to rationalize in terms of either a "barrier" to the "dispersal" of adults and/or larvae, or vicariant patterns tied to Pacific Plate boundaries (Springer, 1982). Synphobranchids occur commonly as far north as the Galapagos Islands, and an adult *H. bathybius* has been collected off the tip of Baja California (Castle, 1964). They occur as far east as Hawaii and other points along the mid-Pacific seamount chain and line island system. However, despite extensive trawling and submersible operations off California to Washington, demersal stages of *Synphobranchius* have not been captured or observed. This parallels somewhat the situation with *Bathysaurus* and *Bathypterois*. Like the "macristium" postlarva of *Bathysaurus*, the leptocephalus larvae of synphobranchids are also potentially long-lived and susceptible to long-distance transport via oceanic currents (Bruun, 1937). While no synphobranchid larvae been reported off the U.S. West Coast, a few pelagic postlarvae of *Bathysaurus* have been collected (Sulak et al., 1985), along with a few adults (Stein and Butler, 1972) demonstrating that at least occasional dispersal into the area does occur. Thus, any hypothesized mid-Pacific watermass "barrier" would be unsatisfactory in explaining zoogeographic limitations. Indeed, a number of deep demersal fish taxa with pelagic larvae and multi-ocean distributions successfully bridge the North Pacific, including the ophiidiids *Spectrunculus grandis* (Nielsen and Hureau, 1980) and *Abyssobrotula galathea* (Nielsen, 1977), the notacanthid *Polyacanthonotus challengerii* (Crabtree et al., 1985), the morid genus *Antimora* (Small, 1981), and the macrourid *Coryphaenoides armatus*. The distributions of the synphobranchids *S. brevidorsalis*, *S. affinis*, *I. arx*, *I. brunneus*, and *S. parasitica* bridge the vast expanse of the South Pacific (Figs. 12–15, 17), again indicating a general ability to disperse across open ocean distances equally as great as found in the Pacific north of the Equator. The curious absence of most Synphobranchidae and many other dominant bathyal/abyssal fish taxa from the northeastern Pacific remains an intriguing enigma. The answer may relate to dif-

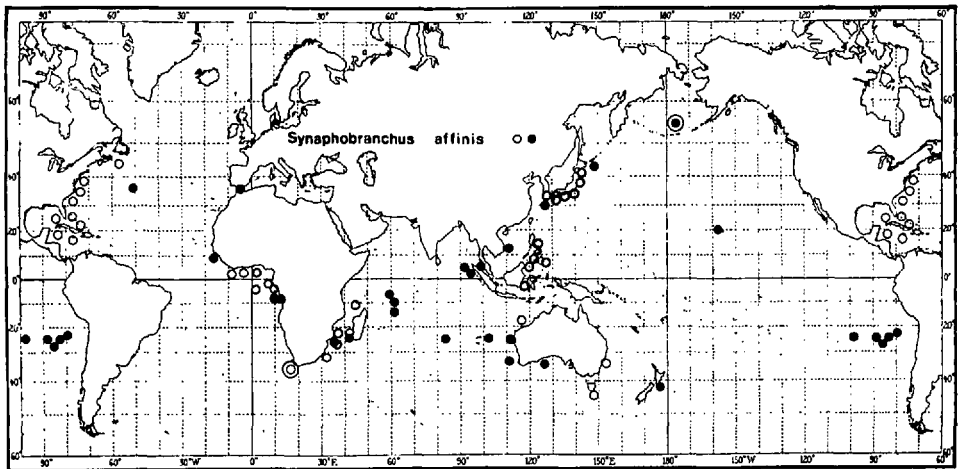


Figure 13. Distribution of *Synaphobranchus affinis*. Solid symbols = Russian records; open symbols = other records; encircled symbol = records with approximate locality data only.

ferential success in adaptation of demersal stages to peculiar ecological conditions, relative to established and well diversified demersal taxa (e.g., Cyclopteridae, Scorpaenidae, Macrouridae). Similarly, the absence of certain widely distributed synaphobranchid species from the Caribbean may also relate to differential success in regional adaptation (Anderson et al., 1985), or to differences in relative availability of preferred prey (Crabtree et al., 1991).

Despite uneven sampling effort, some conclusions can be drawn for the Synaphobranchidae. First, except for a few records, the family is generally confined to tropical and temperate latitudes. The general exclusion of synaphobranchids from high latitudes is probably due to temperature limitations upon the pelagic leptocephalus larvae, rather than limits upon the adult stage. As Castle (1964) has noted, deep Arctic bottom temperatures lie within the thermal tolerance range of the adults of individual synaphobranchid species like *H. bathybius*.

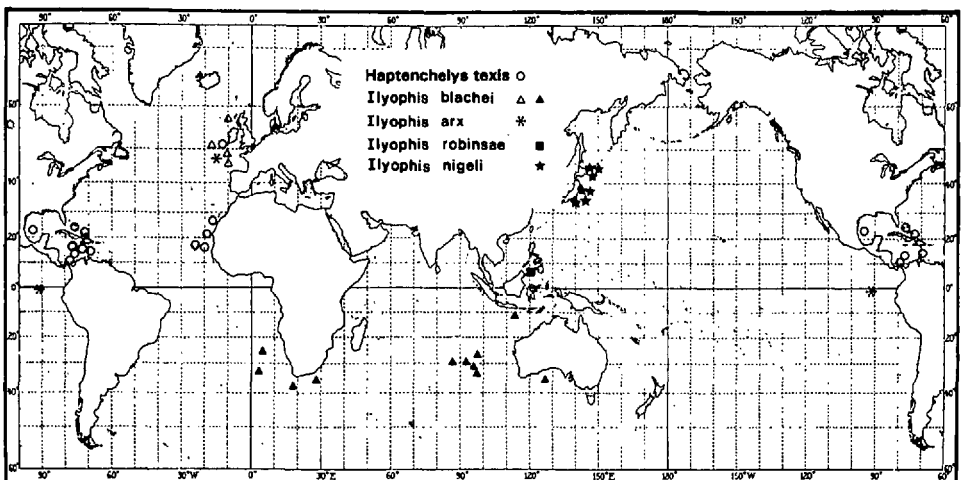


Figure 14. Distributions of *Haptenchelys texis*, *Ilyophis blachei*, *I. arx*, *I. robinsae* n. sp., and *I. nigeli* n. sp. Solid symbols = Russian records; open symbols = other records.

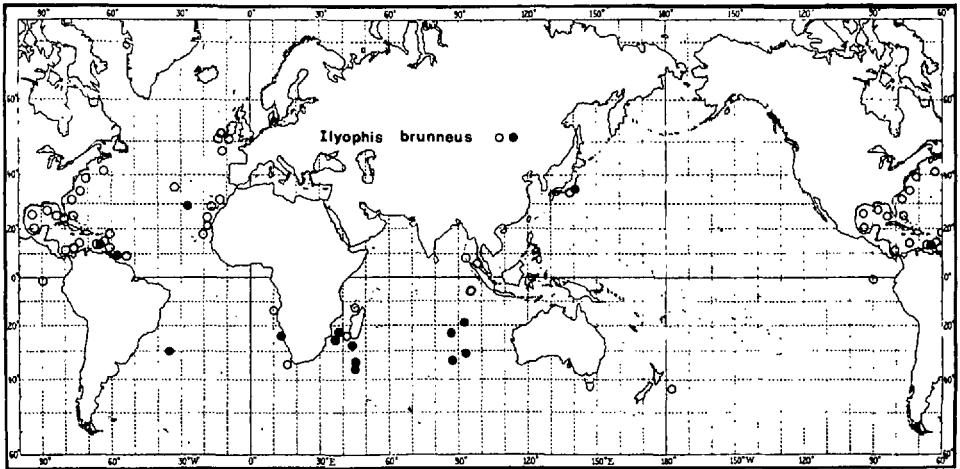


Figure 15. Distribution of *Ilyophis brunneus*. Solid symbols = Russian records; open symbols = other records.

Aside from the northeastern Pacific, synphobranchids are also notably absent from the Mediterranean, and apparently from the Arabian Sea and Bay of Bengal. Absence from the Mediterranean, which has a depauperate demersal deep-sea fish fauna, is not surprising. The exceptionally high bottom temperatures in the Mediterranean (uniformly exceeding 11.5°C) lie outside the known tolerance range (-1.1 to 11.3°C) of all species of synphobranchids. Apparent absence from the Arabian Sea (except for one capture of *S. brevidorsalis*) and Bay of Bengal may be an artifact of limited sampling effort.

Robins and Robins (1989) argue that ocean surface or near-surface conditions control the distribution of synphobranchid species via limits on the pelagic leptocephalus larval stage. However, in the best known species, *S. kaupii*, the latitudinal range of demersal stages (Fig. 11) in the Atlantic extends broadly beyond the rather restricted range of leptocephalus larvae (Bruun, 1937, fig. 8). It is apparent from the broad, multi-ocean distributions displayed by many bathyal and abyssal synphobranchids, halosaurids, and notacanthids (all with leptocephalus larvae) that species distributions in these taxa are not closely dependent on larval stage limitations. The life histories of synphobranchid eels may parallel those of *Anguilla* and *Conger*, requiring long-distance return to very localized ancestral spawning grounds (Schmidt, 1931; Bruun, 1937). Adult longevity (i.e., time available for long-distance dispersal of individuals prior to return spawning migration) may impose limits on species distribution and relative abundance at increasing distances from a small number of spawning grounds within individual ocean basins. Differential adaptation among synphobranchid species to energy availability (Sulak, 1982) or to other ecological parameters may also determine whether or not a particular species occurs frequently and/or abundantly in a particular region.

Synopsis of the limited total vertebral count data for four broadly distributed synphobranchine species indicates substantial regional meristic differentiation in some species (Table 1). Indeed, it is possible that *S. affinis* and *S. oregoni*, for example, may represent composite species. However, vertebral count differences among regional populations could arise in response to different temperatures or food availability during larval development. A more extensive systematic study of vertebral counts will be necessary to adequately define geographic differenti-

ation. Biochemical systematics techniques may be required to determine if vertebral count differentiation is ecophenotypic or genetically-based.

Distributional Synopsis by Species

Synaphobranchus affinis is known from 188 captures (1520 specimens) at depths of 290–2,334 m and bottom temperatures of 3.3 to 11.3° C (50 records). It displays perhaps the most general distribution (Fig. 13) of any synaphobranchid, occurring widely across tropical and temperate latitudes (44° N to 42° S), including numerous records from the southeastern Pacific. However, the species is rare in the northeastern Atlantic and southwestern Pacific, and unknown in the southwestern Atlantic, northwestern Indian Ocean, and northeastern Pacific (except for a single Bering Sea record, above 50° N). As in other members of the genus, *S. affinis* is otherwise absent from polar waters. In the northwestern Atlantic where the species is best known, it is a dominant faunal component between latitudes 35–39° N, but much less important at lower latitudes (Sulak, 1982). Vertebral count data (Table 1) suggest differentiation between North Pacific specimens and specimens from all other areas. Although broadly eurybathic, *S. affinis* is primarily a middle to lower slope inhabitant; all but 16 depth records lie between 500–1,500 m.

Synaphobranchus kaupii is known from 493 captures (10,346 specimens) at depths of 274–2,869 m and bottom temperatures of –1.1 to 9.8 ° C (268 records). The species distribution (Fig. 11) is similar to that of *S. affinis*, except that *S. kaupii* is common and abundant in the northeastern Atlantic (Gordon and Duncan, 1985), while in the Pacific it is known only from the northwestern rim. Its range in the Atlantic also extends much farther north (to 67° N). The species is a dominant component of the Atlantic demersal deep-sea fish fauna (Haedrich et al., 1975, 1980; Sulak, 1982; Gordon and Duncan, 1985; Merrett and Domanski, 1985; Sulak and Ross, 1993) primarily at temperate latitudes. When more completely known, the distribution of *S. kaupii* may prove to be essentially antitropical, a pattern typical of several synaphobranchid species. Occupying a somewhat deeper depth center than *S. affinis*, *S. kaupii* is a middle slope to upper rise inhabitant; all but 21 records lie between 400–2200 m. Among available total vertebral counts, little regional differentiation is apparent (Table 1) within this species.

Synaphobranchus brevidorsalis is known from 222 captures (3,318 specimens) at depths of 230–2,960 m and bottom temperatures of 2.4 to 11.3° C (175 records). The species is confined to lower latitudes (37° N to 29° S) than *S. affinis* or *S. kaupii*, and is much more patchily distributed (Fig. 12). Centered on a slightly deeper depth range (all but 14 records between 1,000–2,500 m) and narrower temperature range (all but three records between 2.4 to 5.2° C) than that of *S. kaupii*, *S. brevidorsalis* tends to replace the former on the lower slope in the Bahamas (Sulak, 1982). Although abundant in Bahamas deeps (Sulak, 1982), *S. brevidorsalis* is curiously absent from the Caribbean (Anderson et al., 1985), and is rare in the fauna off the coast of the states of the middle Atlantic (Crabtree et al., 1991). Its patchy success may relate to functional replacement of congeners within zones of lower food availability (Sulak, 1982; Anderson et al., 1985). This flabby species may be particularly well adapted to low food availability, and may depend more heavily on scavenging (Crabtree et al., 1991) than does *S. kaupii*. Robins and Robins (1989) give total vertebral counts of 130–140 for western North Atlantic specimens, compared to our counts of 131–136 for 10 eastern Indian Ocean specimens. However, Robins and Robins (1989) indicate that spec-

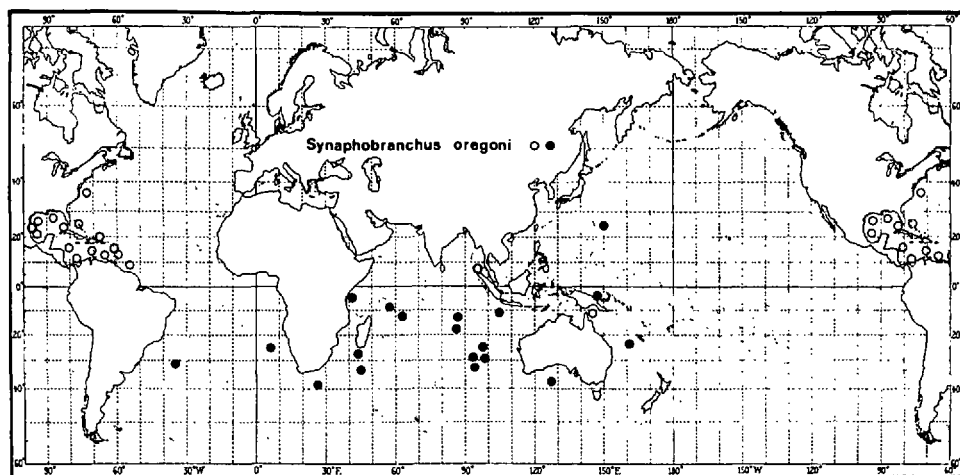


Figure 16. Distribution of *Synphobranchus oregoni*. Solid symbols = Russian records; open symbols = other records.

imens from off Japan may have counts as low as 124–125, suggesting some geographic differentiation.

Synphobranchus oregoni is known from 104 captures (597 specimens) at depths of 512–1,900 m and bottom temperatures of 3.2 to 6.7° C (5 records). Like *S. brevidorsalis*, *S. oregoni* is confined to warm temperate to tropical latitudes (37° N to 39° S), but displays a curious distribution pattern (Fig. 16). It occurs broadly throughout the Pan-Caribbean region, and across the southern Atlantic, Indian and southwestern Pacific oceans (unknown from the central and southeastern Pacific). The pattern is fundamentally congruent with that displayed in the demersal deep-sea chlorophthalmid species complex *Bathypterois phenax* + *B. atricolor*, the geographic species-pairs *B. viridensis* + *B. guentheri* (Sulak, 1977a; Shcherbachev, 1981), and *Ipnops murrayi* + *I. agassizi* (Shcherbachev, 1981). These parallels suggest the possibility of an unresolved geographic species pair within *S. oregoni*, as herein understood. Western North Atlantic specimens display notably higher total vertebral counts, 142–148 (Robins, 1971), than Indo-Pacific specimens from Russian collections, 127–137 (Table 1), suggesting a substantial level of geographic differentiation.

Diastobranchus capensis in our study is known from 40 captures (87 specimens) at depths of 183–1,750 m; no bottom temperature data are available. Extensive additional captures have recently been reported without specific locality data from off southeastern Australia at 800–1,200 m (Koslow et al., 1994). A nearly circum-austral distribution pattern (excluding the central or eastern South Pacific) characterizes *D. capensis* (Fig. 11). Again, this pattern closely parallels that displayed by deep-dwelling chlorophthalmids *Bathypterois filiferus* and *Bathysauropsis gracilis* (Shcherbachev, 1981). All but six depth records lie between 800–1,400 m, indicating *D. capensis* is primarily an inhabitant of the lower slope. Given similar depth and latitude preferences, and a high probability of similar diets, this species appears to be the Southern Hemisphere ecological counterpart of *S. kaupii*. Indeed, their geographic distributions are largely complementary (Fig. 11). Relative to other synphobranchine species, both have exceptionally firm musculature, suggesting equivalent adaptation for powerful swimming and active foraging.

Histiobranchus bathybius is known from 51 captures (220 specimens) at depths of 731–4,700 m and bottom temperatures of 1.4 to 5.8° C (10 records). It displays the broadest latitudinal range of any synaphobranchid (62° N to 48° S) (Fig. 12), and is one of only three species occasionally found in polar waters. A circum-global distribution pattern characterizes *H. bathybius*, although only two records exist for the eastern Pacific (a single capture in the Bering Sea, another off Mexico). All but 12 records lie between 2,000–3,500 m, indicating that *H. bathybius* is primarily an inhabitant of the continental rise. Eastern South Atlantic and southwestern Indian Ocean specimens display a range of total vertebral counts, 122–131, lower than specimens from other regions (Table 1). However, the total number of radiographs available for synopsis is insufficient to evaluate potential geographic differentiation.

Histiobranchus bruuni is known from only three captures (five specimens) at depths of 4,198–4,958 m. Bottom temperature data coordinated with captures are unavailable. However, temperatures estimated from capture localities and depths are 1.2 to 1.5° C. Although captures are few, *H. bruuni* appears to occupy a very restricted distribution (45° to 55° S) in abyssal basins between Australia-New Zealand and Antarctica (Fig. 12). These basins may prove to be a unique area of endemism for a small set of abyssal species, in contrast to the more general abyssal pattern of very broad species distributions. Two abyssal chlorophthalmid species, *Bathypterois oddi* and *B. longicauda*, may also be restricted to the same area (Sulak, 1977a), perhaps due to stenothermal adaptation to unusually and consistently cold sub-Antarctic bottom waters.

Haptenchelys texis is known from 16 captures (21 specimens) at depths of 2,161–4,086 m and bottom temperatures of 2.7 to 3.5° C (6 records). This is a continental rise inhabitant known so far only from the North Atlantic (10° N to 50° N) (Fig. 14), where its distribution appears to follow an amphi-Atlantic pattern. It would not be surprising to discover that *H. texis* has a multi-ocean distribution, as has been proven to be true in the synaphobranchid *I. arx* and other "rare" continental rise species.

Simenchelys parasitica is known from 143 captures (588 specimens) at depths of 136–2,620 m and bottom temperatures of 3.5 to 9.2° C (57 records). It displays a bi-temperate (44° N to 42° S) distribution (Fig. 17) with absence from low latitudes (15° N to 20° S). The species occurs broadly in the North Atlantic, then circum-australly, and along western rim of the North Pacific. Disjunction across tropical latitudes suggests that population differentiation should be investigated. Although broadly eurybathic, *S. parasitica* is primarily a middle to lower slope inhabitant occupying a fairly narrow temperature range. All but nine depth records lie on the middle and lower slope between 500–1,800 m; 56 of 57 temperature records lie between 3.5 and 5.2° C.

Ilyophis brunneus is known from 210 captures (665 specimens) at depths of 450–3,120 m and bottom temperatures of 2.9 to 4.6° C (116 records). The species is broadly distributed between latitudes 51° N to 42° S, but is basically anti-tropical with a tropical zone of disjunction along the Equator (Fig. 15). This geographic and bathymetric pattern is closely similar to that of *S. parasitica* (Fig. 17). All but 12 *I. brunneus* depth records lie on the lower slope and upper rise between 750–2,700 m. Abundant on the slope and rise in the Bahamas, *I. brunneus* appears restricted to bathyal depths in the Caribbean (Anderson et al., 1985). In the Pacific, the species is known from one locality east of New Zealand and one locality near the Galapagos Islands (Fig. 15), the apparent gap between these distant locales again a likely demonstration of our lack of knowledge of the Pacific fauna.

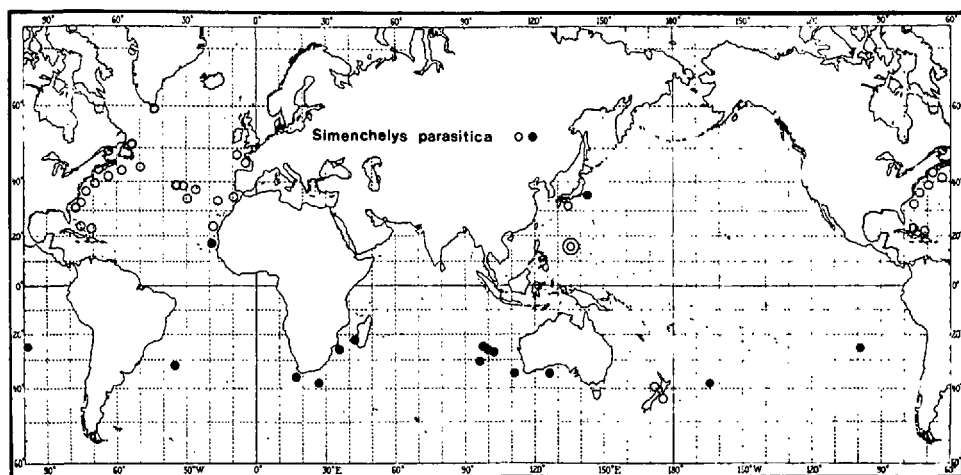


Figure 17. Distribution of *Simenchelys parasitica*. Solid symbols = Russian records; open symbols = other records; encircled symbol = record with approximate locality data only.

Ilyophis blachei is now represented by 27 captures (34 specimens), including 15 localities from Russian exploration in the Southern Hemisphere (Fig. 14). It is known from depths of 580–2,023 m, bottom temperatures of 3.8 to 6.3° C (eight records), and latitudes between 57° N and 36° S). The distribution pattern for *I. blachei* is austral (southeastern Atlantic and southern Indian Ocean) at temperate latitudes, with a curiously disjunct population in the temperate northeastern Atlantic (Fig. 14). When more records become available, this unusual distribution may resolve itself into an anti-tropical, bi-temperate pattern. Vertebral counts for 13 northeastern Atlantic specimens (Saldanha and Merrett, 1982) are 179–188, showing but slight difference in range from our counts of 177–183 for eight Southern Hemisphere specimens.

Ilyophis arx is known from only three captures (seven specimens) at depths of 1,790–3,225 m, bottom temperatures of 3.8 to 4.5° C (two records), and latitudes of 50° N to 2° S). The distribution of *I. arx*, with two records from the temperate northeastern Atlantic and one from the equatorial eastern Pacific, displays how poorly developed is our knowledge of distributions of demersal deep-sea fishes, particularly those of the inadequately explored continental rise. Our analysis of the holotype and one northeastern Atlantic specimen of *I. arx* concurs with Merrett and Saldanha's (1985) determination that Atlantic and Pacific specimens all pertain to a single species. This disagrees with Robins and Robins (1989) suggestion that northeastern Atlantic specimens must represent a distinct species. Such widely disparate locality records for a rare continental rise taxon are not limited to the synphobranchid *I. arx*. A parallel pattern, for example, has been reported by Sulak (1977b) for the halosaurid *Halosaurus attenuatus*.

Ilyophis nigeli, newly described herein, is known from only eight captures (nine specimens) at depths of 700–1,780 m. Bottom temperature data are unavailable. Thus far, *I. nigeli* is known only from the Pacific slope off Japan at latitudes 44° N to 35° N (Fig. 14).

Ilyophis robinsae, newly described herein, is described from the type locality (one specimen) at a depth of 4,800 m, and latitude 8° N (Fig. 14).

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Appendix. Primary taxonomic study material for species of synphobranchid eels of the genera *Diastobranchus*, *Haptenchelys*, *Histiobranchus*, *Ilyophis*, *Simenchelys*, and *Synphobranchus*. A complete list of all accepted distributional records of species of these genera through 1991 is available from the senior author. Institutional or collection acronyms follow Leviton et al. (1985), except for one addition and two modifications: IOS = Institute of Oceanographic Sciences Deacon Laboratory, Wormley, England; ZIL = Zoological Institute, Leningrad; ZMMU = Zoological Museum, University of Moscow. Lots without identification numbers are uncataloged field or museum lots. Supplementary museum lot designations in parentheses indicate split lots from the same locality, or previous museum lot designations. Additional supplementary data in parentheses are given if no field number was assigned, or if locality data are approximate based on a place name designation only. Research vessel abbreviations are as follows: AA = USS ALBATROSS, AB = ANTON BRUUN, AC = A. T. CAMERON, AK = AKADEMIK KURCHATOV, AL = ALBA, AR = ADLER, AT = ARTEMIDA, AX = AKADEMIK KELDISH, C = HMS CHALLENGER, CI = COLUMBUS ISELIN, CM = CHRONOMETR, DA = DANA, DC = DISCOVERY COLLECTION vessels, DM = DMITRY MENDELEYEV, EA = EASTWARD, EK = EKVATOR, EV = EVRIKA, FI = FIOLENT, GA = GADUS ATLANTICA, GE = GERAKL, GT = GALATHEA, GY = GYRE, H = L'HIRONDELLE, IK = IKTIANDR, IN = HMIS INVESTIGATOR, KD = KARA-DAG, LH = LADY HAMMOND, MD = MIS DALNY, MT = MIS TIKIL, MU = MIS UNIONI, N = ALFRED NEEDLER, OC = OCEANUS, OD = ODDISEY, P = PILLSBURY, PE = PERSEI III, PK = PULKOVSKII MERIDIAN, PM = PROF. MESSIATSEV, PO = POLTAVA, PR = PROFESSOR, SA = SALEHARD, SH = SHANTAR, SS = SESKAR, ST = PROF. STOKMAN, T = TALISMAN, TH = THOR, TO = TIKIOKEANSKII, VI = VITIAZ, ZK = ZVEZDA KRYMA. Some cruise numbers have been coded for brevity (original cruise designation available upon request).

Museum ID#	Vessel cruise & sta. #	# Spec.	Museum ID#	Vessel cruise & sta. #	# Spec.
<i>Diastobranchus capensis</i>			ARC 8704392	OC 108 (ARC 8704464)	3
ZMMU 14442	FI 4	1	IOAN	VI 2220	1
IOAN	DM 16-1281	1	<i>Histiobranchus bruuni</i>		
ZMMU 16271	PM 12	7	ZMUC P32444	GT 601	1
ZIL 22975	AL 387	1	<i>Ilyophis arx</i>		
IOAN	PK 9	1	ANSP 133808	AB 16619A	4
ZIL	EK	2	IOS	DC 50517	1
ZMMU 16654	DM 1373	17	<i>Ilyophis blachei</i>		
IOAN	TO 45	1	IOAN	FI 4-162	1
ZMMU 14443	FI 3-38	1	ZMMU 15712	FI 5-82	1
ZMMU 14441	FI 4-26	1	IOAN	DM 16-1373	1
ARC 8909795	VI 17-2742	2	ZMMU 15207	FI 3 126	1
ZMMU 15659	PM 8-22	1	ZMMU 15745	ZK 6-136	1
IOAN	VI 17-2671	2	IOAN	KD 8-114	1
IOAN	VI 17-2672	1	ZMMU 15692	FI 9-39	1
IOAN	VI 17-2673	1	ZMMU 15711	FI 9-43	1
ZMMU 15763	PM 7-141	1	ZMMU 15706	FI 9-40	2
ZMMU 15764	PM 7-135	1	ZMMU 15746	PM 7-24	1
ZMMU	PM 2-35	1	ZMMU 15748	PM 7-25	2
ZMMU 13693	PM 15-41	1	ZMMU 15744	PM 7-20	2
ZMMU 15698	FI 9-38	1	USNM 315198	IK 4-42 (& IOAN)	4
ZMMU 15710	FI 9-37	1	ZMMU 15661	PM 8-69	1
ZMMU	PM 2-14	1	ZMMU 15747	PM 7-46	1
ZMMU 15716	PM 7-26	3	<i>Ilyophis brunneus</i>		
ZIL 42352		2	IOAN	VI 17-2742	3
ZMMU 43823	EV (24-10-1975)	1	IOAN	VI 17-2674	1
ZMMU 15658	PM 8-70	1	IOAN	VI 17-2673	2
ZIL 45384	MT 28	1	ZMMU 15921	PM 7-22	2
ZIL	SA (Whale Ridge)	1	ZMMU	PM 2-26	1
<i>Haptenchelys texis</i>			ZMMU 14462	ZK 6-180	1
ANSP 133812	P 346	1	ZMMU 13671	PM 2-22	1
IOS	DC 8682#5	2	IOAN	VI 17-2666	1
<i>Histiobranchus bathybius</i>			IOAN	VI 17-2629	1
ZMMU 14458	FI 5-98	1	ZIL 43822	EV	1
IOAN	DM 16-1367	1	IOAN	VI 17-2621	1
ZIL	DM 1388 (Acc. 209-976)	7	ZMMU 15737	PM 7-17	1
IOAN	VI 17-2772 (AMS)	2	ZMUC P32453	GT 110	1
ARC 8909793	VI 17-2779	22	ZMUC P32451	GT 324	1
ARC 8909397	VI 17-2639 (IOAN)	2	ZMMU 17952	AK 14-1209	1
ZIL 11716	C 237	9	ZIL 49225	SH 116	1
IOAN	VI 2-80	1	ARC 8704395	OC 106	1
ARC 8704390	OC 109	1			

Appendix. Continued

Museum ID#	Vessel cruise & sta. #	# Spec.
<i>Ilyophis nigeli</i>		
ZIL 49224	SH 116	1
ZIL 45767	MD 18	1
ZIL 45275	GE 135	1
ZIL 48482	EK 206	2
ZIL 45274	GE 66	1
ZIL 48481	EK 166	1
ZMMU 17952	VI 2078	1
ZIL 48483	PR 97	1
<i>Ilyophis robbinsae</i>		
ZMMU 14759	VI 57-7237	1
<i>Simenchelys parasitica</i>		
ZMMU 17057	TO 42	1
ZMMU 13693	PM 2-14	1
IOAN	IK 4-51	1
IOAN	ST 18-1996	1
ZMMU 17057	TO 42	1
ZIL 42325		2
ZIL 42351		3
ZMMU	DM 1373	1
ZMMU 14440	FI 4-91	2
ZMMU	PM 2-14	1
IOAN	IK 4-51	1
ZMMU 15738	PM 7 43	2
IOAN	VI 17-26	1
ZMMU 15697	FI 9-27	1
ZMMU 16622	ZK 268	1
ZIL	EK 240	4
ARC 8704449	OC 106	2
ARC 8705148	LH 127-6	1
ARC 8705194	N 53-72	1
ARC 8602934	LH 127-48	2
ARC 8705141	N 69-66	1
ARC 8705145	LH 127-51	3
ARC 8705147	N 53-43	4
ARC 9111074	N 109-57	2
ARC 9111073	N 109-24	1
ARC 8705482	N 69-18	1
ARC 8600720	GY 86-708	1
ARC 8602933	LH 140-39	1
<i>Synaphobranchus affinis</i>		
ZIL 37518	AR 2	1
ARC 8602969	N 19-31	2
IOAN	DM 16-1373	100
IOAN	DM 16-1388	7
IOAN	ST 1956	32
ZMMU 16613	PM 510	1
IOAN	ST 1908	1
IOAN	ST 1945	6
IOAN	ST 1994	1
ZMUC P32454	GT 203	1
IOAN	ST 1976	3
IOAN	ST 1967	121
IOAN	VI 17-2631	3
ARC 8909502	VI 17-2629	3
IOAN	ST 1897	3
ARC 8909498	VI 17-2637	4
IOAN	ST 1996	15
IOAN	ST 2018	3
IOAN	ST 2019	1
IOAN	IK 5-53	1
IOAN	IK 5-52	1
IOAN	ST 1995	15

Appendix. Continued

Museum ID#	Vessel cruise & sta. #	# Spec.
IOAN	ST 1885	4
IOAN	ST 1884	4
IOAN	VI 31-4564	1
IOAN	ST 1876	11
IOAN	IK 6-11	3
IOAN	VI 17-2652	2
IOAN	ST 1864	1
ZMMU 15707	FI 9-50	3
IOAN	VI 17-2820	3
ZMMU 14044	FI FAO-1-94	1
IOAN	FI FAO-1-95	1
ZMMU 15713	PM 7-7	2
ZMMU 16612	PT 68	1
IOAN	OD 20	1
IOAN	VI 3768	2
ZIL 45100		1
IOAN	VI 2-80	1
ARC 8704460	OC 106	8
IOAN	VI 2078	1
ARC 8602967	N 53-23	2
ZIL 42415	SS	1
<i>Synaphobranchus brevidorsalis</i>		
ZIL 22411		1
ZIL 42351		3
IOAN	VI 17-2629 (& AMS)	14
IOAN	VI 17-2653	1
ARC 8909794	VI 17-2815 (& IOAN)	10
ZMMU 14461	ZK 6-5	2
ARC 8909796	CI C012 (& VIMS)	11
IOAN	MU 49	1
ZSI F1141	IN 338	1
<i>Synaphobranchus kaupii</i>		
ZIL	PR	9
ZIL	SH 1975	1
ZIL	AT 6-279	1
ZIL	EK	2
ZIL 36145		1
ZIL 40691	PE 2-138	2
ZMMU 14460	FI 5-92	1
ZMMU 14459	FI 5-86	3
ZMMU 16616	PO 424	1
ZIL 42351		3
IOAN	VI 17-2653	1
ZMMU 15708	FI 5 (Saya de Maya)	3
ZMMU 14046	FI FAO-1	1
ZMMU 15699	FI FAO-1 95	2
IOAN	AK 36-3705	1
ZMMU	ZK 268	2
ZMMU 16615	ZK 155	2
ZMMU 16573	ZK 153	1
ZMMU 16617	ZK 143	2
ZMMU 16614	ZK 311	3
ZIL 42325	(NE Atlantic)	2
ZMMU 1212	T 41 (MNHN)	9
ZMUC P32867	EA 20094	1
ZIL	EK 240	1
ZIL 9852	H 219	2
ARC 8704427	OC 105	210
ARC 8704469	OC 101	18
ZIL	ER 205	4
ARC 8705146	N 5-56	12
ARC 8600341	AC 103-96	1
ARC 8602967	N 53-23	2
ARC 8705140	N 69-18 (ARC 8705144)	7

Appendix. Continued

Museum ID#	Vessel cruise & sta. #	# Spec.
ZMMU 10550	SV 17-253	2
ARC 8705143	N 53-12	1
IOAN	CM 8 (Ithurup Island)	2
ARC 8909756	GA 37-838	22
ARC 8808424	GA 37-853	2
ARC 8705142	N 19-31	10
ARC 8600705	GY 86-701	1
ARC 8809702	GA 51-960	4
ARC 8808432	GA 51-961	1
ARC 8600704	GY 86-708	21
ARC 8600702	GY 86-702	7
ARC 8600701	GY 86-703	12
ARC 9111077	N 109-7	1
ARC 8600703	GY 86-704	38
ZMUC P32514	TH 80	4
ZIL	AT	1
IOAN	AX 4-445	2
ARC 8704247	GA 129-0402	1
ARC 8704043	GA 129-2624	1
ARC 8704017	GA 129-1917 (& NMC)	12
ARC 8704027	GA 129-3028	2
ARC 8704061	GA 129-3735	3
ARC 8704243	GA 129-6765	3
ZMUC P32865	DA 10018	2
<i>Synaphobranchus oregoni</i>		
ZMMU	DM 1373	16
IOAN	VI 17-2671	5
IOAN	VI 17-2672	1
IOAN	VI 17-2772	1
ZMMU 13699	PM 2-26	1
ZMMU 16624	PM 2-20	1
ZMMU 15701	FI 9-37	2
ZMMU 13693	PM 2-14	1
ZMMU 15721	FI 9-40	1
ZMMU 15702	FI 7-24	1
IOAN	JK 4-50	2
ZMMU 15703	FI 9-28	2
IOAN	VI 17-2666	2
ZMMU 15695	FI 9-27	1
ZMMU	PM 8-69	1
ZIL 45385	MT 28	3
ZMMU 15704	PM 7-11	2
ZMMU 15705	PM 7-10	5
ZMMU 15707	FI 9-50 (ZMMU 15696)	3
AMS 20920-002		1
ZMMU 15694	PM 7-5	15
ZMMU 15691	FI 9-21	1
IOAN	VI 54-6732 (USNM)	1
IOAN	VI 17-2815	9
ZMMU 15713	FI 9-52	1
IOAN	DM 18-1542	3
ZMUC P32449	GT 241	1
ZMUC P32450	GT 324	1
IOAN	MU 50	1
USNM 46153	AA 239	1